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FOSSIL ENALIARCTINE PINNIPEDS (MAMMALIA: OTARIIDAE)
FROM PYRAMID HILL, KERN COUNTY, CALIFORNIA

By Lawrence G. Barnes



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FOSSIL ENALIARCTINE PINNIPEDS (MAMMALIA: OTARIIDAE) FROM PYRAMID HILL, KERN COUNTY, CALIFORNIA^{1, 2}

By Lawrence G. Barnes³

ABSTRACT: Including *Enaliarctos mealsi*, a total of three named fossil species of enaliarctine pinnipeds in the carnivore family Otariidae are now known by skulls from latest Oligocene to earliest Miocene rocks in California. Two of these species are new: *Enaliarctos mitchelli*, new species, and *Pinnarctidion bishopi*, new genus and species. Most of the published fossils are from two strata in the lower part of the Pyramid Hill Sand Member of the Jewett Sand that is exposed at Pyramid Hill in the southern part of the San Joaquin Valley in Kern County. Increasing aquatic adaptation relative to *E. mealsi* and adaptive and phylogenetic diversity within the subfamily Enaliarctinae are demonstrated by these new taxa. The two known genera have different skull proportions and dental and basicranial characters.

In the past, *E. mealsi* has been thought to be a possible otariine (modern sea lions, fur seals) ancestor. *P. bishopi*, on the other hand, shares many characters with extinct species of *Allodesmus*, particularly with *A. packardii*. Therefore, the subfamily Enaliarctinae, as defined in this study, apparently gave rise to at least two other otariid subfamilies; the Allodesminae and the Otariinae. The other otariid subfamilies (Desmatophocinae, Imagotariinae, and Odobeninae) also may have been derived from the Enaliarctinae, but there is no published paleontological proof of this. Rather than classify each enaliarctine genus within its apparently descendent subfamily, I propose the continued recognition of one basal group, the subfamily Enaliarctinae. This classification joins in one subfamily the primitive otariids that have a similar stage of evolution. I believe that the morphological diversity and apparent phylogenetic relationships of the six above named subfamilies warrant their inclusion in only one carnivore family, the Otariidae.

INTRODUCTION

Our knowledge of the evolutionary history of sea lions, fur seals, and walruses has increased greatly in recent years. Most of the new evolutionary information derives from fossil evidence and has been recently reviewed by Mitchell (1968, 1975), Repenning (1975, 1976), Repenning and Tedford (1977), and by Tedford (1976). These reviews include phylogenies, classifications, and a cladistic analysis. Such interpretations of the fossil record of these animals were not attempted prior to the mid-1960's. The classification of the sea lions, fur seals, walruses, and their extinct relatives is presently a matter of controversy, as evidenced by the diversity of opinions in recent studies.

Most mammalogists have traditionally placed the modern walruses in the family Odobenidae, and the modern sea lions and fur seals in the family Otariidae. A majority of authors have recognized that these two families are more closely related to each other than either is to the true seals of the family Phocidae. In recognition of this closer relationship, the Otariidae and Odobenidae are therefore classified by some authors together in the superfamily Otarioidea. Most of the named fossil pinnipeds showing affinities with sea lions or walruses were placed by their original describers in either the Otariidae or the Odobenidae. Early departures from this classification were the naming of the

families Desmatophocidae Hay 1930 and Allodesmidae Kellogg 1931. These two families were not generally accepted, however.

Mitchell (1968) emphasized that most known fossil otariid species were not clearly members of either modern lineage, but belonged to other lineages, some of which shared characters in various combinations both with modern sea lions and with walruses. His classification had six subfamilies, including the subfamily Odobeninae (walruses) as a new rank, in one family, the Otariidae. A seventh subfamily, the primitive Enaliarctinae, was later added to the family Otariidae (Mitchell and Tedford 1973;

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Mitchell 1975). In their studies, Repenning and Tedford have recognized most of the subfamilies in Mitchell's classifications, but have put them in four different families. They kept the Odobenidae and Otariidae at family rank and recognized two additional families; the Enaliarctidae and the Desmatophocidae (Repenning 1975, 1976; Repenning and Tedford 1977). Tedford's (1976) cladistically inspired classification is still different in placing *Enaliarctos* Mitchell and Tedford 1973 in the family Enaliarctidae and the Odobeninae (and presumably some or all of the other subfamilies recognized by Mitchell (1968)) in the family Otariidae.

The classification that I adopt in this study (see p. 38) consists of one family, the Otariidae, that includes the subfamilies Enaliarctinae, Otariinae, Desmatophocinae, Allodesminae, Imagotariinae, and Odobeninae. It is a middle ground between the above-mentioned classifications, but is closest to that of Mitchell (1968, 1975), and does not include Dusignathinae.

Enaliarctos mealsi Mitchell and Tedford 1973 is geologically the oldest and morphologically the most primitive named fossil otariid. Authors (Mitchell and Tedford 1973; Repenning 1975, 1976; Repenning and Tedford 1977; Tedford 1976), therefore, have considered the monotypic subfamily Enaliarctinae (or in some classifications family Enaliarctidae) to be ancestral to most or all of the later otariids, and to be transitional in morphology between fissiped and otariid pinniped carnivores. Mitchell (1975:19), Repenning (1975:29; 1976:376–377), Ray (1976:429), Tedford (1976:369), and Repenning and Tedford (1977:77, 79) have indicated that other fossils referable to the Enaliarctinae exist in collections but are not yet described.

The holotype and referred specimens of *Enaliarctos mealsi* were collected from rocks of late Oligocene or early Miocene age at Pyramid Hill which is in Kern County in the southeast part of California's San Joaquin Valley (see Addicott 1970:fig. 3; Mitchell and Tedford 1973:figs. 1, 4). The purpose of the present paper is to describe additional fossils of *Enaliarctos mealsi*, skull parts of a new species of *Enaliarctos*, and skull parts of another, more advanced new genus and species of pinniped from the same localities and rock sequence at Pyramid Hill, to compare them with those specimens studied by Mitchell and Tedford (1973), and to place them in evolutionary and stratigraphic perspective. The fossils from Pyramid Hill document the first described wide diversity of primitive otariids in late Oligocene or early Miocene time.

Many postcranial bones of primitive otariids have been collected from rocks at Pyramid Hill and elsewhere. Until associated or articulated skeletons are described, however, the referral of any of these isolated postcranial bones to any of the species based upon skulls will be tenuous. Some additional bones will be described by myself and Edward Mitchell in a separate study.

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Peggy Zeadow, Daphne Cowan, and Doris Pickering aided in manuscript preparation. The photographs were prepared by Armando Solis (Figs. 2, 14–21), and Lawrence Reynolds (Figs. 3, 4, 6, 8) of the Natural History Museum of Los Angeles County. Some of the drawings were prepared by David Cook (Figs. 7, 9, 10) and by J. Patricia Lufkin (Figs. 5, 11–13), both staff artists of the University of California Department of Paleontology, Berkeley. The remaining illustrations are by the author.

ABBREVIATIONS

Institutional acronyms for specimens cited in the text are:

- CIT: California Institute of Technology, Pasadena; collections and records now held by Natural History Museum of Los Angeles County.
- LACM: Natural History Museum of Los Angeles County, Section of Vertebrate Paleontology, Los Angeles, California, U.S.A.
- SBMNH: Santa Barbara Museum of Natural History, Santa Barbara, California, U.S.A.
- UCMP: University of California Museum of Paleontology, Berkeley, California, U.S.A.

METHODS

Most of the mammal bones from the Pyramid Hill Sand Member of the Jewett Sand are in concretionary sandstone that is harder than the enclosed bone. Mechanical preparation using pneumatic, air-abrasive, and grinding tools is satisfactory for removing bulk matrix, but destroys the outer surface of the bone. Acetic acid ($\text{CH}_3\text{CO}_2\text{H}$) or formic acid (HCO_2H) in a dilute aqueous solution (10 to 20 percent) dissolves the sandstone matrix but not the bone. The bone surface that is exposed by acid must be periodically removed from the solution, rinsed with water, neutralized with a base, rinsed again with water, dried thoroughly, and coated with diluted resin or with a plastic cement similarly diluted with acetone.

A pinniped palate described in this paper (UCMP 80943), was found as the sole remaining part of a shattered skull that was at one time complete and enclosed in a nodule. The teeth and ventral surface of the palate were buried in the matrix and the visible surface was the bone of the dorsal surface of the palate within the nasal chamber. Polyester resin and fiberglass cloth were applied to the exposed broken surface of the bone and acetic acid and air-abrasive tools were used to remove the matrix from the occlusal surface of the palate. As a result, the prepared specimen consists of a thin layer of bone laminated on a fiberglass and resin base.

Most of the skull measurements given in Table 3 were made following the instructions given by Sivertsen (1954:18–20) and by Barnes (1972:3). Mitchell and Tedford (1973:table 2) also used several of the measurements explained by Sivertsen, and

some additional ones. Some of the values I recorded for measurements of the specimens of *Enaliarctos mealsi* differ from those recorded by Mitchell and Tedford, and are indicated by an asterisk in my Table 3. For these questionable values, I have attempted to duplicate the measurement method shown in Sivertsen's (1954) figures 5 through 7. For example, I have measured the zygomatic root of the maxilla, Sivertsen's (1954:20, fig. 6) measurement 14, across the narrowest span to the ventral lip of the infraorbital foramen. Measurements not defined by Sivertsen, such as the length of the tooth row from C to M², the width between the infraorbital foramina, the point of greatest intertemporal constriction, the width of the palate across the anterior roots of P⁴, and the greatest width of the anterior nares are explained in Barnes 1972:fig. 1. The post-palatal length (palatal notch to basion), used in this study and by Mitchell and Tedford (1973), was considered by Sivertsen (1954:20) to be unserviceable, but is useful as a measure of anteroposterior length for the mostly fragmentary enaliarctine skulls at hand.

Among the measurements not previously defined by Sivertsen or Barnes, and used in this report and/or by Mitchell and Tedford (1973), the post-palatal length is measured from the basion to the posterior point of Sivertsen's (1954:fig.6) measurement 10, and the paroccipital width is measured across the lateral extremities of the paroccipital processes. The width across the occipital condyles is measured from the lateral edges of the articular surfaces. Measurements of the nares, foramen magnum, and infraorbital foramen are straightforward. With the exceptions of the measurement from the basion to the anterior end of the zygomatic root and the width of the zygomatic root of the maxilla, all measurements are in sagittal, frontal, vertical, or transverse planes of the skull. Most of the estimated transverse measurements are half-skull measurements multiplied by two.

GEOLOGIC AND PALEONTOLOGIC CONTEXT

The Tertiary marine rocks that are exposed in Kern County just west of California's Sierra Nevada contain a sequence of invertebrate and vertebrate fossil assemblages that is of great importance to studies of marine vertebrate evolution and of Tertiary chronology. The marine rocks crop out in low hills in a northwest to southeast trending belt between the Sierra Nevada and the area of the city of Bakersfield (Addicott 1970:fig. 1). Addicott (1970) has provided a recent review of the Tertiary marine rock units in the region. Mitchell and Tedford (1973) have also discussed the regional geology, with emphasis upon the marine rocks that are exposed at Pyramid Hill.

The specimens that were used in the original description of the oldest named fossil otariid pinniped, *Enaliarctos mealsi* Mitchell and Tedford 1973, were collected at Pyramid Hill (see Addicott 1970:fig. 3; Mitchell and Tedford 1973:fig. 1) from the basal part of the Pyramid Hill Sand Member of the Jewett Sand. This is the oldest marine rock unit exposed on the south face of Pyramid Hill where it unconformably overlies the non-marine Walker Formation (Addicott 1970:10; Mitchell and Tedford 1973:fig. 4). Elsewhere in the Bakersfield area, the Pyramid Hill Sand Member either is separated from the underlying Walker Formation by the intervening Vedder Sand, or lies unconformably directly upon the basement complex of the Sierra Nevada (Addicott 1970:9, 12).

With the exception of the isolated teeth, all of the pinniped fossils described in this report were in concretions from Pyramid Hill. Within the lower part of the Pyramid Hill Sand Member of the Jewett Sand at Pyramid Hill, there are two fossiliferous, concentration-bearing beds (Mitchell and Tedford 1973:figs. 2, 4; Fig. 1, this report).

The age and depositional differences between these two beds are not yet clearly understood, but indications are that their fossil species compositions are different. I therefore consider it very important to distinguish from which bed each fossil was derived. The lowest of these two beds (including localities LACM 1603, 1626, 1627, UCMP V7032) is at the very base of the Pyramid Hill Sand Member, contains pebbles, rounded black chert grains, angular quartz clasts, and is referred to as the "grit zone" by some geologists (Addicott 1970:12). The Pyramid Hill Local Fauna named and characterized by Mitchell and Tedford (1973:216, 268–272) should be strictly limited to the fossil assemblage from the "grit zone."

I concur with Mitchell and Tedford (1973:220–221, fig. 2) that the holotype (LACM 4321) of *Enaliarctos mealsi*, found loose on the hillside, probably originally came from the lower concretion bed (LACM locality 1627) in the "grit zone." The coarse sandstone that remains within the skull is typical of concretions from this lower bed. The isolated teeth referred to *Enaliarctos mealsi* by Mitchell and Tedford (1973) and in this report, and those identified only as *Enaliarctos* sp. in this report, were collected from a nearby locality toward the west end of Pyramid Hill (LACM locality 1626 = UCMP locality V7032) which is also in the "grit zone" (Mitchell and Tedford 1973:fig. 2, table 4). The skull (LACM [CIT] 5303) that was referred to *Enaliarctos mealsi* by Mitchell and Tedford (1973:229) is in a finer matrix such as is found in higher beds, but the color of the bone is characteristic of those from the lower bed. The exact source of this referred specimen is still uncertain, but I believe it was derived from the lower bed. Its museum locality is given as CIT locality 481, a designation which records that the specimen was discovered as a loose item at the base of Pyramid Hill with no source bed implied. Fossils in UCMP that have the locality designation V6618 were found under similar circumstances.

The upper fossiliferous, concretion-bearing bed (LACM locality 1628 = UCMP locality V6916) on the south face of Pyramid Hill is 40 to 50 feet stratigraphically above the lower "grit zone" (Mitchell and Tedford 1973:figs. 2, 4), and the concretions in this upper bed are characteristically finer grained, stained reddish-brown on the outside by iron oxide, and are gray internally (Addicott 1970:12; and personal observations). The holotype skull (UCMP 86334) of *Pinnarctidion bishopi*, new genus and species, was collected *in situ* from this upper bed in a concretion fitting the above description.

The endocranial cast (LACM [CIT] 5302) referred to *Enaliarctos mealsi* by Mitchell and Tedford (1973:229–232) and referred herein on new morphological evidence to *Pinnarctidion bishopi*, new genus and species, and the holotype (UCMP 100391) and paratype (UCMP 80943) of *Enaliarctos mitchelli*, new species, have bone color and matrix characteristic of the upper concretion bed, and are presumed to have rolled down Pyramid Hill from that level (= LACM locality 1628 = UCMP locality V6916). Their listed museum locality numbers (CIT 481 = UCMP V6618), however, indicate that they were discovered as loose specimens on the lower slopes of Pyramid Hill.

The interstitial matrix surrounding the fine-grained concretions

in the upper bed is a very different coarse quartz sand containing mollusk shells and other fossils. Some of the bones are exposed at the surfaces of the enclosing concretions and appear to have become so exposed by erosion. In the case of the holotype of *Pinnarctidion bishopi*, new genus and species, the right zygomatic arch and the end of the rostrum were exposed at the surface of the enclosing concretion and worn away, but the coarser matrix surrounding the concretion was in contact with the exposed bone surface. These facts suggest that the fine-grained, bone-bearing concretions were derived from some other, probably older source rock, and were re-deposited in coarse sand when the upper concretion-bearing bed was laid down. At the present time, it is not known how much older than the surrounding coarse sand matrix these bone-bearing concretions might be, but I believe they are undoubtedly younger than the lower basal "grit zone." Fossils from this upper bed should not be included as part of the Pyramid Hill Local Fauna of Mitchell and Tedford (1973).

In summary (see Fig. 1), the stratigraphic distribution of fossil pinnipeds now known from the Pyramid Hill Sand Member of the Jewett Sand exposed at Pyramid Hill is as follows: *Enaliarctos mealsi* is probably from the lowest fossil-bearing horizon (LACM locality 1627) in the "grit zone." The holotype of *Pinnarctidion bishopi*, new genus and species, is definitely from the upper fossil-bearing concretion bed (LACM locality 1628 = UCMP locality V6916). Based on lithology and bone color the referred specimen of that species and the holotype and paratype of *Enaliarctos mitchelli*, new species, were probably originally from the same upper bed. Bones in the upper bed were probably redeposited when that bed was formed, but probably are none-the-less still geologically younger than the basal "grit zone."

Addicott (1970:33–34, fig. 2) and Mitchell and Tedford (1973:214–217, 220, 272) agreed by stating that based on paleontological evidence the age of the Pyramid Hill Sand Member of the Jewett Sand is early Miocene. This is roughly consistent with ages and correlations derived from various sources, but should not be accepted without some qualification. For example, based on its contained fossil mollusks, the Jewett Sand falls within the "Vaqueros" provisional California provincial molluscan stage as used by Addicott (1972:8–10; 1976), which he called early Miocene in the California chronology. Mitchell and Tedford (1973:272) believed that teeth of the horse, *Anchitherium* sp., from the "grit zone" are most similar to those of *A. agatense* (Osborn 1918) of Arikareean age from the Harrison Formation of Nebraska, and, therefore, they (1973:217, 220, fig. 3) correlated the "grit zone" with the Arikareean North American Land Mammal Age. Evernden, Savage, Curtis, and James (1964:165) reported a radiometric date of 21.3 million years from the Agate Ash in the Harrison Formation.

The holotype of the odontocete *Argyrosetus joaquinensis* Kellogg 1932 undoubtedly was derived from the Pyramid Hill Sand Member of the Jewett Sand (Mitchell and Tedford 1973:268; Barnes 1976:325) despite information presented by Kellogg (1932:1) that it was derived from the older "Vedder zone." The matrix adhering to the holotype of *A. joaquinensis* is similar to that on the holotype of *Enaliarctos mealsi*, and I conclude that both specimens are from the basal "grit zone" of the Jewett Sand. Most of the molluscan species listed by Kellogg (1932:1) from the type locality of *A. joaquinensis*, are also listed by Addicott (1972:9) as representative of the "Vaqueros" provisional California provincial molluscan stage. The type species of *Argy-*

rosetus Lydekker 1894, *A. patagonicus* Lydekker 1894, is from the early Miocene Patagonian marine formation in Argentina. I have compared (Barnes 1976:325, 335) the grade of evolution of the aggregate cetacean assemblage from the Jewett Sand with that of odontocetes from the early Miocene deposits at Belluno, Italy (see Dal Piaz 1977 for summary of cetacean assemblage there).

The Jewett Sand has been assigned by various workers to the upper Zemorrian, the upper Zemorrian and lower Saucian, or the Saucian foraminiferal stages (see Addicott 1970:33 for summary). There is some disagreement, however, among authors as to how these foraminiferal stages correlate with the European sequence and with the radiometric time scale. Evernden, et al. (1964:167) and Turner (1970:97, 100–101, table 1, fig. 4) showed the Zemorrian-Saucian boundary equivalent to the late Arikareean Land Mammal Age and at about 22 or 22.5 million years ago, but avoided epoch correlations. Berggren and Van Couvering (1974:fig. 12) showed the Oligocene-Miocene epoch boundary at 22.5 million years ago. Bandy and Ingle (1970:fig. 2), however, showed the Oligocene-Miocene boundary between 24.1 and 25 million years ago and also correlative with the Zemorrian-Saucian boundary. Lipps (1967:fig. 4) placed the Zemorrian-Saucian boundary slightly younger than the Oligocene-Miocene boundary. Most consistent information, therefore is that the Zemorrian-Saucian boundary is about 22.5 million years old and correlates with the Oligocene-Miocene boundary. The foraminiferal stage assignments for the Jewett Sand quoted above, therefore, would allow no more accurate epoch assignment for this rock unit than latest Oligocene to early Miocene. This would be roughly 21 to 23 million years ago (Turner 1970, Berggren and Van Couvering 1974:fig. 12).

Mitchell and Tedford (1973) discussed the other fossils found associated in the same rock sequence with the fossil otariids at Pyramid Hill. Additionally, Bishop (1969) has commented on the diverse shark assemblages in both the lower "grit zone" and the upper concretion-bearing bed.

Wilson (1935) described fossil bones of primitive pinnipeds that were collected from outcrops of the Jewett Sand (Addicott 1970:9) northwest of Pyramid Hill and west of the small town of Woody. Some of these bones were identified by Wilson as phocids (true seals). In their survey of previously described primitive pinniped bones, Mitchell and Tedford (1973:267–268, 272–275) suggested that Wilson's phocid identifications were incorrect and that all the bones belonged to primitive otariid pinnipeds of an "otter like" grade of evolution. Mitchell (1966:20, pl. 24) and Barnes and Mitchell (1975:34) have also discussed the identities of some of the bones originally described by Wilson.

It is my belief that there is presently no firm evidence for or against the statement that the exposures of the Jewett Sand near Woody differ chronologically from the exposures at Pyramid Hill (as suggested by Mitchell and Tedford 1973:216–217, 272). The absence of documented invertebrate fossils in the outcrops near Woody will make it necessary to rely on stratigraphic and vertebrate fossil evidence to resolve the problem. The possibility does exist that some of the pinniped bones comprising the Woody Local Fauna of Mitchell and Tedford (1973), belong to the same species of otariids described in this report. This matter will be investigated in a separate study by Edward Mitchell and myself (in preparation).

The Jewett Sand is overlain by middle and late Miocene rock units that are best exposed farther to the west. These younger,

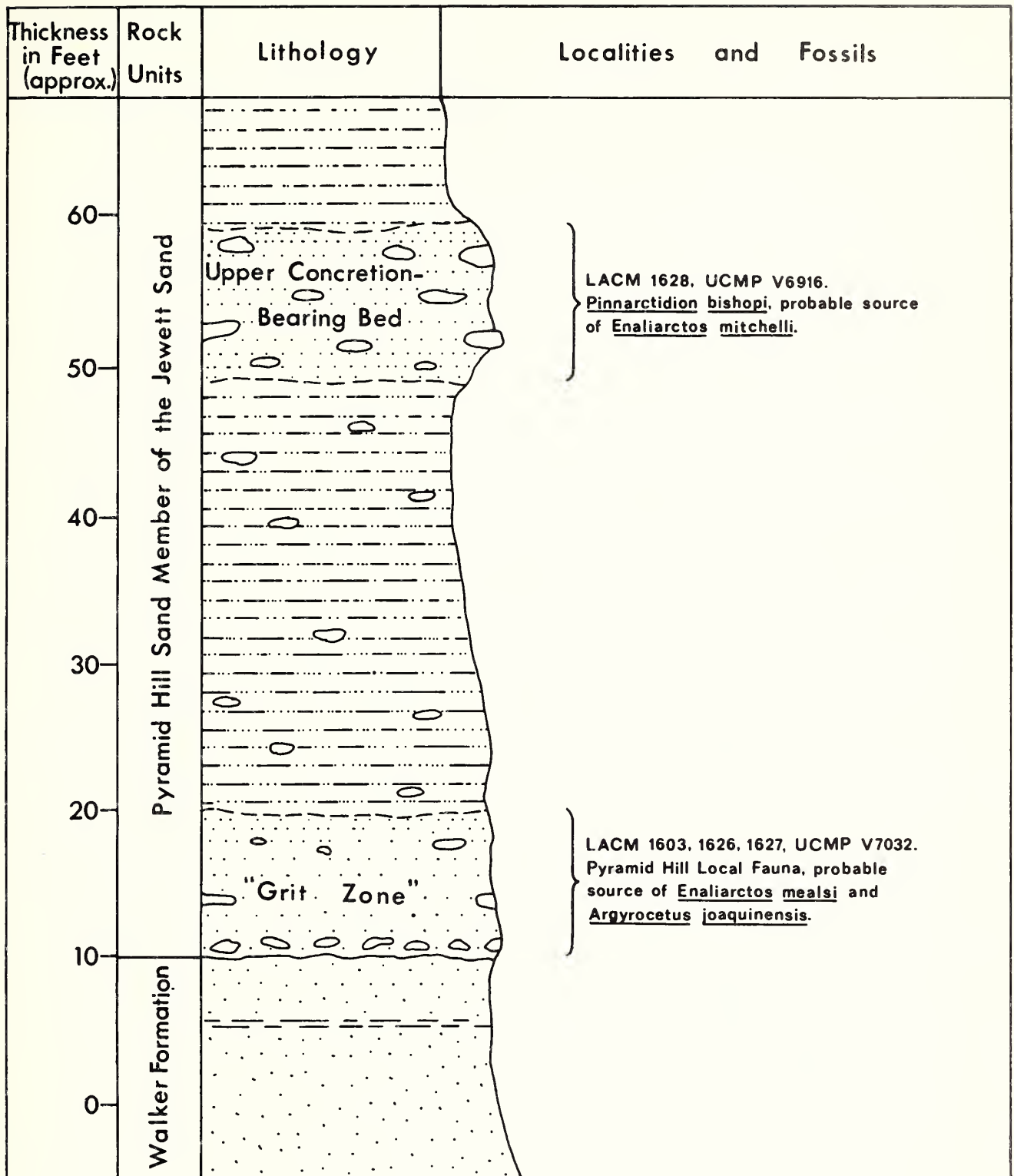


FIGURE 1. Generalized columnar section of the top of the Walker Formation and the base of the Pyramid Hill Sand Member of the Jewett Sand at Pyramid Hill. The sources of fossils, including enaliarctine otariids, and positions of vertebrate fossil localities are shown. (Derived in part from Mitchell and Tedford 1973: figs. 2, 4, table 4; and Addicott 1970.)

overlying rocks include the Round Mountain Silt which contains in its upper part the important Sharktooth Hill Bonebed, the source of abundant marine vertebrate fossils. I have (Barnes 1976, and see literature cited there) summarized the sequence of known fossil cetaceans in these overlying marine rock units and in the Jewett Sand.

SYSTEMATICS

CLASS MAMMALIA Linnaeus 1758

Order CARNIVORA Bowdich 1821

Family Otariidae Gill 1866

Trichechidae Gray 1821:302; invalid, based on *Trichechus* Linnaeus 1766 (walruses), *nec Trichechus* Linnaeus 1758 (manatees, family Trichechidae Gill 1872).

Otariina Gray 1825:340; as a tribe of the family Phocidae, to include *Otaria* Péron 1816.

Otariidae Brookes 1828:37; improperly formed name.

Otariidae Gill 1866:7, 10, (sea lions and fur seals).

Rosmaridae Gill 1866:7, 11, invalid, based on *Rosmarus* Scopoli 1777=*Rosmarus* Brünnich 1772=*Odobenus* Brisson 1762, (walruses).

Odobenidae Allen 1880:5, 17; originally spelled Odobaenidae, emended by Palmer 1904:833 (walruses).

Desmatophocidae Hay 1930:557; for *Desmatophoca oregonensis* Condon 1906, only.

Allodesmidae Kellogg 1931:227; inclusion of *Neotherium mirum* Kellogg 1931 uncertain.

Otariidae, *sensu lato*, Mitchell 1968:1844, including Odobeninae, Desmatophocinae, Allodesminae, etc.

Enaliarctidae, Tedford 1976:367 (caption for fig. 2), 372 (table 1); Repenning 1976:376; including *Enaliarctos* and undescribed taxa.

Enaliarctidae. Arnason 1977:241, ?typographic error.

TYPE GENUS: *Otaria* Péron 1816.

INCLUDED SUBFAMILIES: Enaliarctinae Mitchell and Tedford 1973; Desmatophocinae Hay 1930; Allodesminae Kellogg 1931; Imagotariinae Mitchell 1968; Odobeninae Allen 1880; Otariinae Gill 1866.

Subfamily Enaliarctinae Mitchell and Tedford 1973

Enaliarctinae Mitchell and Tedford 1973:218; Mitchell 1975:19 fig. 1.

"Common Ancestral Group." Repenning 1975:29, fig. 11.

Enaliarctidae, Tedford 1976:367 (caption for fig. 2), 372 (table 1); Repenning 1976:376; Repenning and Tedford 1977:11.

Enaliarctidae. Arnason 1977:241, ?typog. error.

EMENDED DIAGNOSIS OF SUBFAMILY: A subfamily of the family Otariidae differing from Allodesminae, Desmatophocinae, Imagotariinae, Odobeninae and Otariinae by having carnassial teeth and a protocone or a protocone shelf on P⁴, and by having a nasolabialis fossa; differing from Allodesminae, Odobeninae, and Otariinae by having three roots on P⁴, a smooth and inflated bulla, and no large orbital vacuity; differing from Imagotariinae and Odobeninae by having a large paroccipital-mastoid crest; differing from Allodesminae and Otariinae by having a larger tympanic membrane; differing from Desmatophocinae, Imagotariinae, Odobeninae, and Otariinae by having a prominent sulcus on cranium corresponding to pseudosylvian fissure of brain; differing from Odobeninae by having a narrow interorbital region; differing from Allodesminae and Desmatophocinae by having an antorbital process; differing from Odobeninae and Otariinae by having a lacrimal foramen; and differ-

ing from Otariinae by lacking a large supraorbital process of the frontal.

TYPE GENUS: *Enaliarctos* Mitchell and Tedford 1973.

INCLUDED GENERA: *Enaliarctos* Mitchell and Tedford 1973, and *Pinnarctidion*, new genus.

Enaliarctos Mitchell and Tedford 1973

Enaliarctos Mitchell and Tedford 1973:218.

EMENDED DIAGNOSIS OF GENUS: A genus of the subfamily Enaliarctinae differing from *Pinnarctidion*, new genus, by having a skull with a wider interorbital region, a smaller orbit, smaller antorbital processes, external openings of optic foramina located relatively higher on the anterior wall of the brain case, narrower and more arched palate, smaller infraorbital palatal plate of maxilla, cheek teeth proportionally larger and more closely spaced, deep embrasure pit for M₁ on palate between P⁴ and M¹, protocone shelf of P⁴ larger and positioned more anteriorly on the tooth, anterolabial corner of M¹ large, posterior narial opening higher and narrower, strut between palate and braincase less concave lateral to pterygoid hamulus, tympanic cavity smaller, paroccipital process smaller and joined to mastoid process by only a low paroccipital-mastoid crest, and occipital condyles nearly parallel in posterior view rather than diverging dorsally.

TYPE SPECIES: *Enaliarctos mealsi* Mitchell and Tedford 1973; type by original designation.

INCLUDED SPECIES: *Enaliarctos mealsi* Mitchell and Tedford 1973, and *Enaliarctos mitchelli*, new species.

Enaliarctos mealsi Mitchell and Tedford 1973

Figures 2a–q, 16a, 18a, 20a

Enaliarctos mealsi Mitchell and Tedford 1973:220.

EMENDED DIAGNOSIS OF SPECIES: A species of *Enaliarctos* differing from *E. mitchelli*, new species, by having a skull with a wider and more dorsoventrally compressed rostrum, a dorsoventrally compressed anterior narial opening that is oval in anterior view, longer nasal bones, zygomatic arches that are more greatly arched at midpoint, ventral surface of zygomatic arch ventral to the infraorbital foramen steeply inclined both anteriorly and laterally, interorbital region relatively wider, at least four pair of posterior palatine foramina instead of one, posterolabial root of P⁴ more widely separated from the other two roots of the same tooth, and the posterior root of M¹ clearly posterior to the posterior margin of the zygomatic arch.

HOLOTYPE: LACM 4321, skull, as described by Mitchell and Tedford 1973, probably from the lower nodule-bearing "grit zone" at Pyramid Hill, LACM locality 1627; collected by Harold S. Meals, 8 January 1961.

PREVIOUSLY REFERRED SPECIMENS: LACM (CIT) 5303, incomplete skull from CIT locality 481, found loose on the slopes of Pyramid Hill and probably derived from the "grit zone," collected by Chester Stock, 1950; LACM 4364, left P⁴ from LACM locality 1626, collected by Harold Meals, March 1961; LACM 4574, left M₁, LACM 4575, left dP₄, and LACM 4576, protocone of left P⁴, all from LACM locality 1626, a locality west of Pyramid Hill correlated with the "grit zone," col-

lected by Joseph F. Arndt, 1960; LACM 17036, left M_1 lacking roots, LACM 20517, right M^2 , both from LACM locality 1626, collected by Richard C. Bishop, 1965.

ADDITIONAL REFERRED SPECIMENS: LACM 4365, left P^3 from LACM locality 1626, collected by Harold Meals, March 1961; LACM 17035, right P_3 or P_4 from LACM locality 1626, collected by Richard C. Bishop; LACM 72383, left M_1 from LACM locality 1626, collected by Michael K. Hammer, 16 January 1966; LACM 72733, left P_3 or P_4 from LACM locality 1626; UCMP 86211, right M^1 from UCMP locality V7032 (=LACM locality 1626), collected by Mark A. Roeder, December 1969.

DISCUSSION: The isolated endocranial cast, LACM (CIT) 5302, previously referred to *Enaliarctos mealsi* by Mitchell and Tedford (1973) is reidentified here as belonging to *Pinnarctidion bishopi*, new genus and species. This restricts the known anatomy of the endocranial cast of *E. mealsi* to the other referred skull, LACM (CIT) 5303. The anterior end of the rostrum of that other skull (LACM [CIT] 5303) referred to *E. mealsi* by Mitchell and Tedford (1973) is broken off in a transverse plane exposing two anteriorly facing holes which Mitchell and Tedford (1973:234, see their fig. 12b) interpreted as alveoli for incisors. The more complete rostrum described herein of *Enaliarctos michelli*, new species, demonstrates that these holes in LACM (CIT) 5303 are not incisor alveoli, but are the cross sections of the incisive foramina (palatine fissures). The alveoli for the incisors were still farther anterior to these foramina. In the reconstructions of *Enaliarctos mealsi* in this study (Figs. 16a, 18a, 20a), the incisive foramina and rostral extremity are based on *E. michelli*. In my previous description of the holotype of *Allo-desmus packardi* Barnes 1972, I also misinterpreted (pp. 48–49) the exposed cross sections of the incisive foramina as medial incisor alveoli. In *A. packardi*, the great lengths of the roots of I^3 are emphasized by the extension of their alveoli posteriorly to a point lateral to the incisive foramina (see Barnes 1972:fig. 18). There is, therefore, no evidence for the existence of only four rather than the usual six upper incisors as I previously restored the skull of *A. packardi* (Barnes 1972:fig. 19). In the present study I have restored the rostrum of *A. packardi* (Fig. 21b) as it is in *A. kernensis* Kellogg 1922. The incisive foramina of *A. kernensis* are small and appear on the palate merged into a single small foramen. This condition in *Allo-desmus* Kellogg 1922 is unique among pinnipeds, which usually have large, paired palatal openings of the incisive foramina as do fissiped carnivores.

Because of the incompleteness of some of the bone in the area of the anterior lacerate foramina (orbital fissures) on the holotype of *E. mealsi*, it is difficult to interpret the precise relationship between the foramen rotundum and the alisphenoid canal. In species of Canidae and Ursidae, the foramen rotundum is in the medial wall of the alisphenoid canal, and is separated from the anterior lacerate foramen by a wide bony septum. In contrast, in the modern Otariinae, the foramen rotundum is merged with the anterior lacerate foramen forming one large aperture, and this is separated from the anterior end of the alisphenoid canal by a bony septum. I judge this to be a derived character. On the left side of the holotype of *E. mealsi*, the posterior wall of the partly obliterated foramen rotundum forms a semicircular notch in the medial wall of the alisphenoid canal. There is, however, no anterior wall of the foramen rotundum that would have separated it from the anterior lacerate foramen, as in canids and ursids. In this respect, *E. mealsi* is intermediate in structure between the

latter and modern otariines, and is morphologically closer to the condition in otariines.

It appears that *E. mealsi* had an inferior petrosal sinus that was enlarged as an embayment in the lateral edge of the basioccipital medial to the bulla which Hunt has shown (1974a:36; 1974b:1038, pl. 1; 1977:830, 837, fig. 2, pls. 1–3) is a structure shared by modern bears and fossil Amphicyonidae. Hunt assumed that the embayment in the extinct amphicyonids served the same function as in modern ursids: to hold an elongate loop of the median branch of the internal carotid artery. Both the holotype (LACM 4321) and referred specimen (LACM [CIT] 5303) of *E. mealsi* show evidence of a relatively small embayment in each side of the basioccipital. It is ventrally located within a rounded tuberosity in the probable area of insertion of the rectus capitis ventralis muscle. On the holotype, the tuberosity on the left side is broken through to reveal the sinus (see Mitchell and Tedford 1973:fig. 5a). On the endocast of the referred specimen (see Mitchell and Tedford 1973:fig. 12a) the bone forming the basioccipital tuberosities is mostly broken away to reveal hemispherical, matrix-filled recesses in the basioccipital. Each sinus, lying medial to the petrosal, is approximately 8 mm wide. The left one is larger than the right. Similar sinuses occur in *Allo-desmus packardi* and in *Pinnarctidion bishopi*, new genus and species, and are discussed in further detail under the description of the latter species.

Mitchell and Tedford (1973:228) described the tympanic crest of *E. mealsi* as being of small diameter. This has been cited (Repenning and Tedford 1977:11) as diagnostic for the subfamily Enaliarctinae (=their family Enaliarctidae). Compared with species of the Otariinae and Allodesminae, however, the tympanic crest of *E. mealsi* is of relatively wide diameter. It measures approximately 7 mm across as compared to 9.3 mm by 7.5 mm across in the much larger holotype skull of *Imagotaria downsi* Mitchell 1968 (see also Repenning and Tedford 1977:32).

Mitchell and Tedford (1973:229) described the M^1 of the holotype of *E. mealsi* as having "three roots of which the lingual root is the largest; the labial roots are smaller and crowded together." Repenning and Tedford (1977:11) cited this character as diagnostic for their family Enaliarctidae. I disagree with this interpretation. I base my observations upon the holotype, the referred skull (LACM [CIT] 5303), and a referred isolated right M^1 (UCMP 86211). The M^1 has only two roots. The anterior, labial root is circular in cross section and separate. The remnant of the formerly separate posterior labial root is fused with the likewise formerly separate lingual root which is above the protocone. These two fused roots form one posterolingually placed root that is bilobed in cross section, and has its long cross-sectional axis anterolabial to posterolingual. The root structure of the M^1 in *E. mealsi* is, therefore, homologous with that of the holotype of *Desmatophoca oregonensis* Condon 1906 (see Mitchell 1975:fig. 2) and of a specimen (USNM 184060) referred to *Imagotaria downsi* by Repenning and Tedford (1977:pl. 8, fig. 1), and exemplifies a probable evolutionary step in the development of the two nearly equal-sized roots on the M^1 of some late Cenozoic and Recent species of Otariinae (e.g. Repenning and Tedford 1977: pl. 19, figs. 3, 4; pl. 20; pl. 22, fig. 2; pl. 23, fig. 12).

The M^1 (UCMP 86211) which I refer to *E. mealsi* (Fig. 2j), was collected from the same locality (LACM 1626 = UCMP V7032) as were all the other isolated teeth referred to *E. mealsi* in this report and by Mitchell and Tedford (1973). The structure and proportions of the crown and root of UCMP 86211 cor-

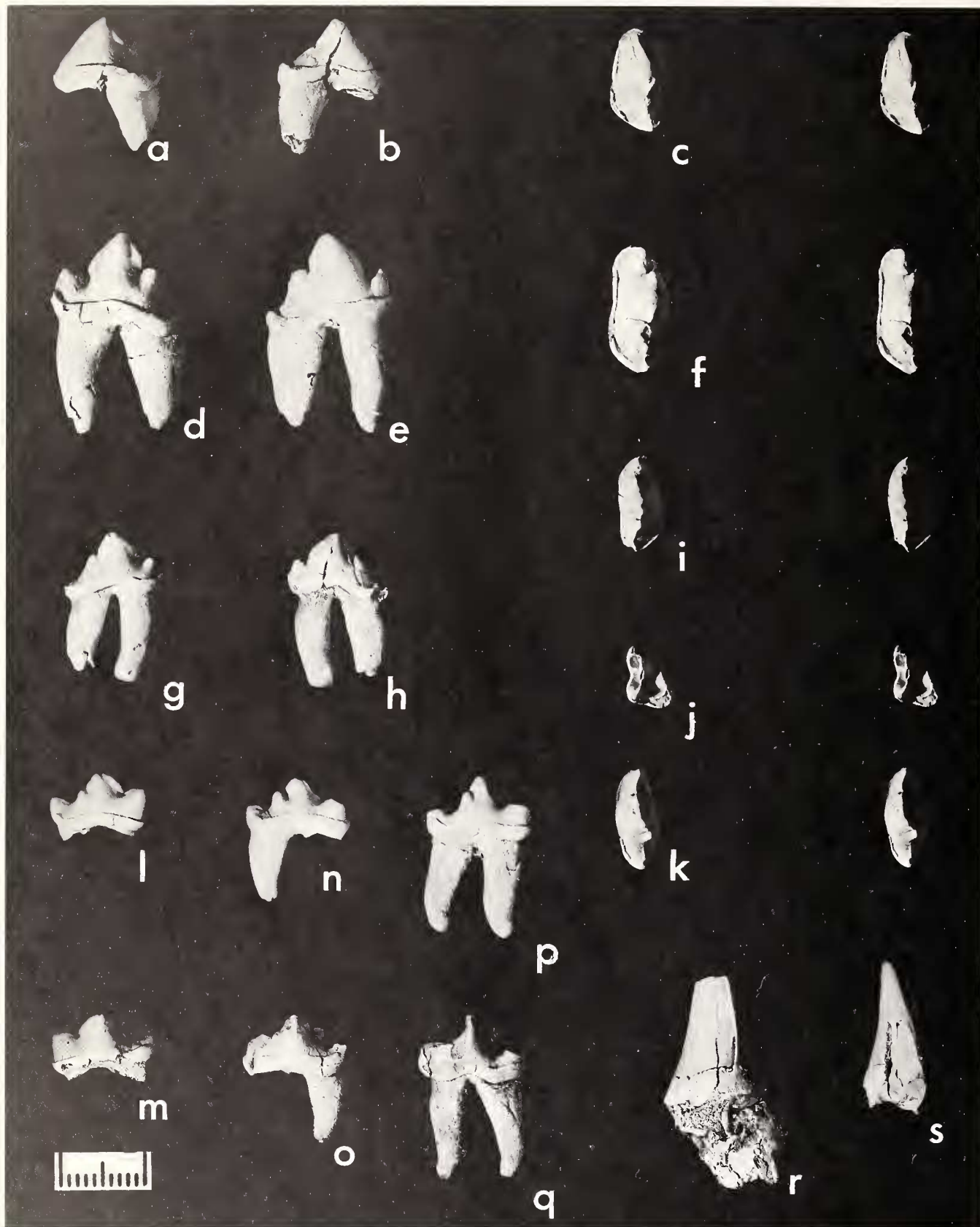


FIGURE 2. *Enaliarctos melesi* Mitchell and Tedford 1973, referred teeth: LACM 4365, left P₃; *a*, lingual view; *b*, labial view; *c*, stereophotograph of occlusal view; LACM 17035, possible right P₃ or P₄ of male; *d*, lingual view; *e*, labial view; *f*, stereophotograph of occlusal view; LACM 72733, possible left P₃ or P₄ of female; *g*, lingual view; *h*, labial view; *i*, stereophotograph of occlusal view; *j*, UCMP 86211, stereophotograph of occlusal view of right M₁; LACM 17036, unworn left M₁ lacking roots; *k*, stereophotograph of occlusal view; *l*, lingual view; *m*, labial view; LACM 72383, moderately worn left M₁ lacking anterior root; *n*, lingual view; *o*, labial view; LACM 4574, heavily worn left M₁; *p*, lingual view; *q*, labial view; *Enaliarctos* sp., referred right upper canine crowns; *r*, LACM 72381, possible male; *s*, LACM 30540, possible female; all from LACM locality 1626 (= UCMP locality V7032); all 1.5 x natural size, scale equals 10 mm.

respond with the left M^1 in the holotype skull, but the isolated tooth is 19 percent smaller than the M^1 in the holotype. Disparate sizes of other specimens referred to *E. mealsi* are noted in the following text.

The referral of an isolated left P^4 with a nearly complete crown (LACM 4364) to *E. mealsi* by Mitchell and Tedford (1973:241–242, fig. 15) was based on similarities between that tooth and the broken fourth premolars in the holotype of the species. The isolated P^4 is about 1 mm shorter than those in the holotype, however, and could have belonged to an individual the size of the referred skull, LACM (CIT) 5303.

The referral by Mitchell and Tedford of the isolated right M^2 (LACM 20517) to the species is supported by the shape of the M^2 alveolus in the holotype skull, but should now be qualified by the knowledge that other enaliarctine species, whose second molars are unknown, occur in the same rock unit.

An isolated tooth (LACM 4365) which I identify as a left P^3 of *E. mealsi* (Figs. 2a–c) probably is from an animal comparable in size to the one that had the left P^4 , LACM 4364. The crown of this P^3 is comprised of one main cusp, the paracone, which is shaped much like the same cusp on the P^4 , LACM 4364. The metacone is reduced to a small cusp on the posterior side of the paracone. A cingulum surrounds the entire crown and is elevated into a posterior cingular cusp. The crown bulges slightly posterolaterally. The posterior root of the tooth is bilobed, and its lingual lobe is above the posterolingual bulge of the crown. The anterior root is broken off, but was originally of smaller diameter than the posterior one. This tooth was apparently used by Mitchell and Tedford (1973) in the preparation of their figure 17, but was not further described or illustrated.

Mitchell and Tedford (1973:242, fig. 16) referred two isolated left M_1 's to *E. mealsi* based upon their proper occlusal relationships with the P^4 and M^1 in the holotype. I have no reason to doubt these referrals, and refer an additional left M_1 , LACM 72383, to the species. All three of these teeth are probably from smaller individuals than the holotype of *E. mealsi*. It is assumed that in life the paraconid of M_1 occluded with the protocone shelf of P^4 and that the hypoconid of M_1 occluded with the protocone shelf of M^1 (see Mitchell and Tedford 1973:242). None of the three referred M_1 's is large enough to occlude with both upper teeth of the holotype at the same time. All three M_1 's are illustrated here (Figs. 2k–q) to show variation. These teeth resemble the M_1 in a mandible (UCMP 114474) from the Skooner Gulch Formation at Point Arena in northern California. I had previously (Barnes in Phillips, Welton, and Welton 1976:152) identified that mandible as an enaliarctine otariid. I now tentatively identify it as *Enaliarctos* sp. based on the similarities between the M_1 in the mandible and the M_1 's referred to *E. mealsi*.

Two isolated cheek teeth (Figs. 2d–i) from Pyramid Hill (LACM locality 1626) resemble the P_3 or P_4 in the same mandible from Point Arena, and I identify them as P_3 or P_4 of *E. mealsi*. These two teeth are of different sizes. The smaller one, LACM 72733, is 25 percent smaller than the other one, LACM 17035, and is the same size as the P_4 in the mandible (UCMP 114474) from Point Arena. Each tooth has two roots and a crown with three main cusps and a lingual and labial cingulum. The cingulum curves dorsally at the middle of both the labial and lingual sides and at the anterior and posterior ends of the crown.

There is a small posterior cingular cusp. The three main cusps are aligned anteroposteriorly and are apparently homologous with the paraconid, protoconid, and metaconid described on the M_1 of *E. mealsi* by Mitchell and Tedford (1973:242). The paraconid is slightly lingual to the anteroposterior axis of the crown. Anteriorly it is confluent with the cingulum and separated from the protoconid by a deep notch. The protoconid is the largest cusp, and in a manner similar to the same cusp on M_1 , is expanded anteriorly by a larger and posteriorly by a smaller narrow crest. The metaconid is close to the posterior side of the protoconid, and is separated from it by a shallow notch. Compared to the paraconid, the metaconid is smaller, but is higher on the tooth.

Mitchell and Tedford (1973:243) discussed the possibility but did not conclude that the size differences between skulls of *E. mealsi* represented sexual dimorphism. Repenning (1976:379) believed there was no evidence for sexual size dimorphism in *E. mealsi* and suggested that the species did not form rookeries as do Recent gregarious otariid species, in which the males are larger than the females. The referred skull, LACM (CIT) 5303, is approximately 9 percent smaller than the holotype. In the foregoing descriptions I have noted size disparities among some of the teeth referred to *E. mealsi*. An isolated M^1 (UCMP 86211, Fig. 2j) is 19 percent smaller than that on the holotype. The three isolated lower first molars are apparently from smaller individuals than the holotype. One referred P_3 or P_4 (LACM 72733) is 25 percent smaller than another (LACM 17035). Since crowns of mammalian teeth do not increase in size during ontogeny, these size ranges may indicate; 1) that more than one species is represented; 2) that *E. mealsi* teeth exhibited wide individual variability; or 3) that the species was sexually size dimorphic. Among Recent species of Otariidae males are larger than females. The present fossil evidence indicates that sexual dimorphism in *E. mealsi* cannot be ruled out.

Regarding the ontogenetic age of the individual animal represented by the holotype skull of *E. mealsi*, I used the sutures and closure values set out for otariids by Sivertsen (1954). Of nine sutures listed by Sivertsen, only one, number IX, the premaxillary-maxillary suture is not preserved on the holotype. All the other eight areas of sutures are preserved and those sutures show maximum closure for values of four each. The suture age of the specimen, therefore, is a minimum of 32, and this would place it in Sivertsen's Group I, adults. The preserved areas of sutures on the referred specimen (LACM [CIT] 5303) indicate essentially equal maturity, except that the interfrontal suture appears not to be entirely closed.

In this paper I present new reconstructions of the skull of *E. mealsi* (Figs. 16a, 18a, and 20a) that are modified from those of Mitchell and Tedford (1973) on the basis of new material and re-interpretations of previously published specimens. The rostral extremity and canine are based upon *E. mitchelli*, new species, but the facial angle is shown as less, based upon the referred specimen of *E. mealsi* (LACM [CIT] 5303). Based upon observations of the holotype (LACM 4321), I have shown a wider lambdoid crest, a smaller paroccipital process, a notch between the articular surfaces of the condyles ventrally, and no notch in the dorsal articular surfaces. I believe the skull originally had a hamular process of the pterygoid as in other fossil and Recent otariids. The P^3 is based on an isolated tooth LACM 4365.

Enaliarctos mitchelli NEW SPECIES

Figures 3–5, 16b, 18b, 20b

DIAGNOSIS OF SPECIES: A species of *Enaliarctos* differing from *Enaliarctos mealsi* by having a skull with a narrower but higher rostrum, a higher anterior narial opening that is more nearly circular in anterior view, shorter nasal bones, zygomatic arches relatively lower on skull and not as greatly arched at midpoint, ventral surface of zygomatic arch ventral to the infraorbital foramen more nearly horizontal and not as steeply inclined anteriorly, interorbital region relatively narrower, only one pair of posterior palatine foramina, roots of P⁴ relatively closer together and forming a nearly equilateral triangle in ventral aspect, both roots of M¹ anterior to posterior margin of zygomatic arch.

HOLOTYPE: UCMP 100391, anterior half of skull, lacking teeth, collected by Dr. Daryl P. Domning, 6 May 1972.

TYPE LOCALITY: UCMP V6618 (=CIT 481). The specimen was found in a loose rock on the south face of Pyramid Hill. It could have fallen from either of the fossiliferous beds upslope, but the fine grained matrix and reddish bone color match those of specimens that are known to have been collected in the upper fossiliferous concretion-bearing bed, LACM 1628 = UCMP V6916. I believe it came from the upper bed.

PARATYPE: UCMP 80943, palatal remnants of a skull, bearing parts of both canines, collected by Dr. J. Howard Hutchison, 18 May 1968. This specimen was collected from the same locality (UCMP V6618) as the holotype. It has similar adhering lithology and is of similar color and is also presumed to have fallen from the upper fossiliferous concretion-bearing bed, UCMP V6916 (=LACM 1628).

ETYMOLOGY: The species is named in honor of Dr. Edward D. Mitchell, Jr., who stimulated renewed interest in the study of fossil otariids, and who collected and studied some of the specimens that are described in this report.

DESCRIPTION: The anterior end of the holotype skull (UCMP 100391) of *Enaliarctos mitchelli* is broken obliquely through the postorbital region (Fig. 3). It was found in one-half of a concretion by Daryl Domning, and was broken by prior human activity or by natural weathering. The posterior part of the skull has not been located at Pyramid Hill. The specimen lacks teeth, and the anterior margin of the rostrum and parts of the incisor alveoli are weathered away. All sutures in the rostrum are fused, including those bordering the nasal bones. The squamosal-jugal suture on the zygomatic arch was, expectedly, not fused. The animal would undoubtedly be considered to be an adult following Sivertsen's (1954) suture age method.

The paratype (UCMP 80943) of *Enaliarctos mitchelli* is a palate discovered by Howard Hutchison adhering to a piece of concretionary matrix after someone had hammered off the rest of the skull. This palate (Figs. 4–5) is not preserved as far anteriorly as is the holotype, but it does contain parts of both canine teeth and is preserved farther posteriorly. It is otherwise directly comparable with the palate of the holotype. As with the holotype of *E. mitchelli*, all the bones of the paratype are fused, obliterating the sutures, and it is also believed to have been from an adult individual.

The following description is partly a composite based upon both the holotype, UCMP 100391, and the paratype, UCMP 80943, which reveal the anatomy of the skull from the tip of the snout to the postorbital area. The skulls of *E. mitchelli* are both smaller than the holotype and referred skulls of *Enaliarctos*

mealsi. With the present specimens, I cannot definitely determine the sex of either skull of *E. mitchelli*, nor determine if this species was sexually dimorphic; however, the small canine of the paratype is consistent for that of a suspected female dimorph (see Table 2).

E. mitchelli differs from *E. mealsi* in having a rostrum that is relatively wider and deeper dorsoventrally. These differences result in its having a more circular external bony narial opening that is higher than wide. The referred skull (LACM [CIT] 5303) of *E. mealsi*, conversely, has a narial opening that is wider than high. The nasal bones of *E. mitchelli* do not extend as far anteriorly nor do they slope as steeply anteroventrally as in *E. mealsi*. Fusion has obscured the sutures surrounding the nasal bones, so it is impossible to see if they contact the frontals posteriorly in the same manner as in *E. mealsi*. Compared with *E. mealsi*, the lateral margins of the narial opening are more steeply inclined in *E. mitchelli*, giving the latter a more blunt snout in lateral view. Its facial angle (as defined by Repenning, Peterson, and Hubbs 1971) is undoubtedly less than in the referred specimen of *E. mealsi*, but the latter is not complete enough to make such a measurement. In *E. mealsi*, the maxillae bow outward on the lateral surfaces of the rostrum more than in *E. mitchelli*. I am convinced that these differences in rostral shape are actual and are not caused by geologic distortion.

The zygomatic arches depart from the skull in a manner different than in *E. mealsi*. Compared with the latter, the anterior end of the zygomatic arch in *E. mitchelli* makes a more acute angle in the horizontal plane where it joins the skull, and curves less dorsally in the sagittal plane at its midpoint. Consequently the postorbital process of the jugal is lower on the skull in *E. mitchelli* (compare Figs. 18a and 18b). The orbit of *E. mitchelli*, therefore, faces more laterally and is positioned lower on the skull than in *E. mealsi*. The nasolabialis fossa, described by Mitchell and Tedford (1973:232, 234) on the side of the snout anterior to the orbit of *E. mealsi*, is more pronounced in *E. mitchelli*. Consistent with the different slope of the lateral surface of the snout, the surface of the nasolabialis fossa is oriented more vertically in *E. mitchelli*. The antorbital process bordering the posterior margin of the fossa, and the eminence at the anterior margin of the fossa are both larger than in *E. mealsi*.

The dorsal surface of the skull upon the nasal bones and anterior to the sagittal crest is flatter, shorter, and proportionally wider than on the skull referred to *E. mealsi*. The intertemporal constriction is relatively narrower, and the sagittal crest, while present, is lower than in *E. mealsi*.

The interorbital septum of the holotype of *E. mitchelli* was entirely broken away prior to fossilization. The lacrimal foramina are also missing. The orbital aperture of the posterior palatine foramen is in a position slightly anterior of its location on the holotype of *E. mealsi*. The opening of the infraorbital foramen within the orbit in *E. mitchelli* is floored by a relatively wider and flatter surface of the maxilla than in the holotype of *E. mealsi*, but is more like the structure in the skull (LACM [CIT] 5303) referred to *E. mealsi* by Mitchell and Tedford (1973).

The palate of both the holotype and paratype of *E. mitchelli* may be compared with both the holotype and referred skull of *E. mealsi*, and there are several differences between the two species. Of the teeth, only P⁴ and M¹ are preserved in place on specimens of *E. mealsi*, and only the canines are known for *E. mitchelli*. Both specimens of *E. mitchelli* are smaller than those of *E. mealsi*. The species are similar in both having heterodont dentition, a

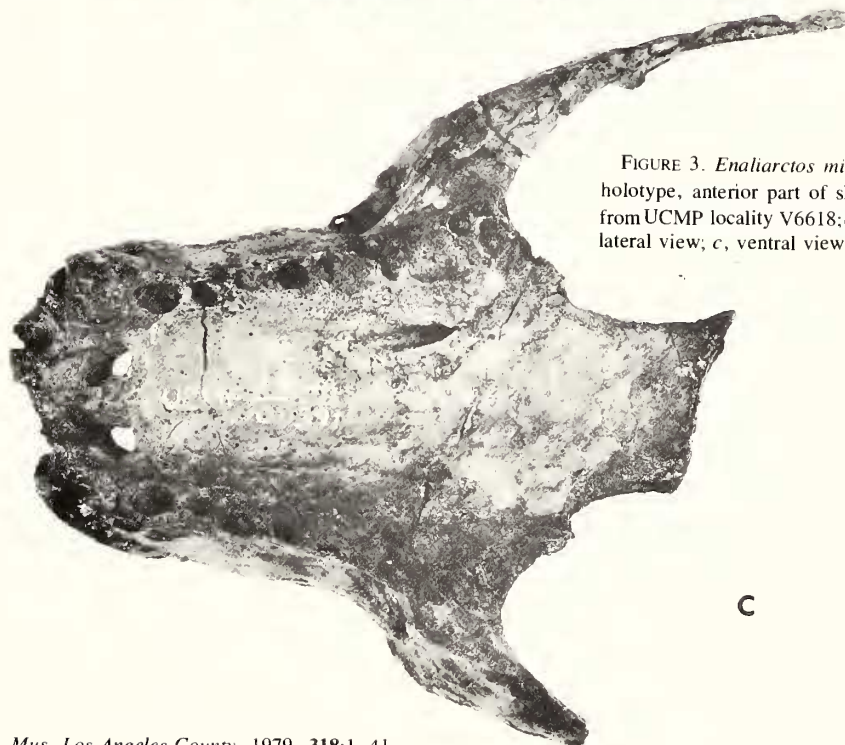
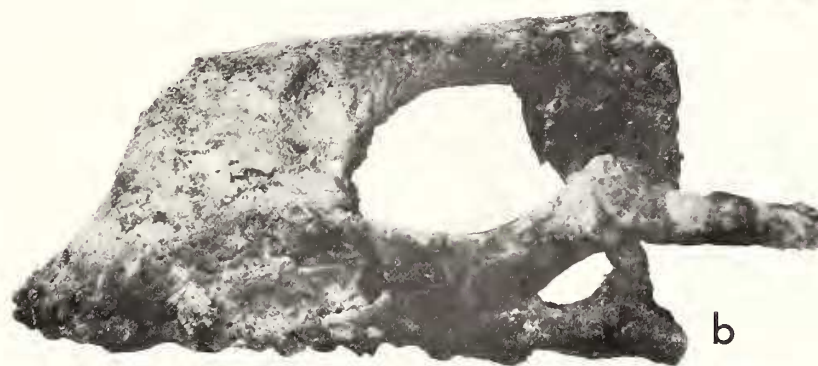
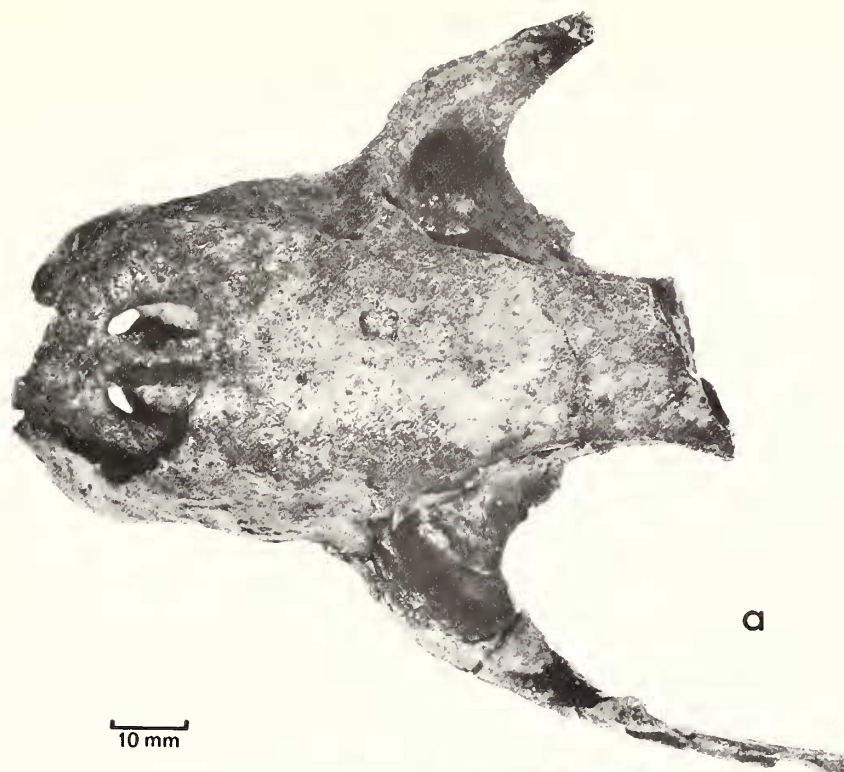


FIGURE 3. *Enaliarctos mitchelli*, new species, holotype, anterior part of skull, UCMP 100391 from UCMP locality V6618; *a*, dorsal view; *b*, left lateral view; *c*, ventral view; natural size.



FIGURE 4. *Enaliarctos mitchelli*, new species, paratype, palate with canines, UCMP 80943 from UCMP locality V6618, ventral view, natural size.

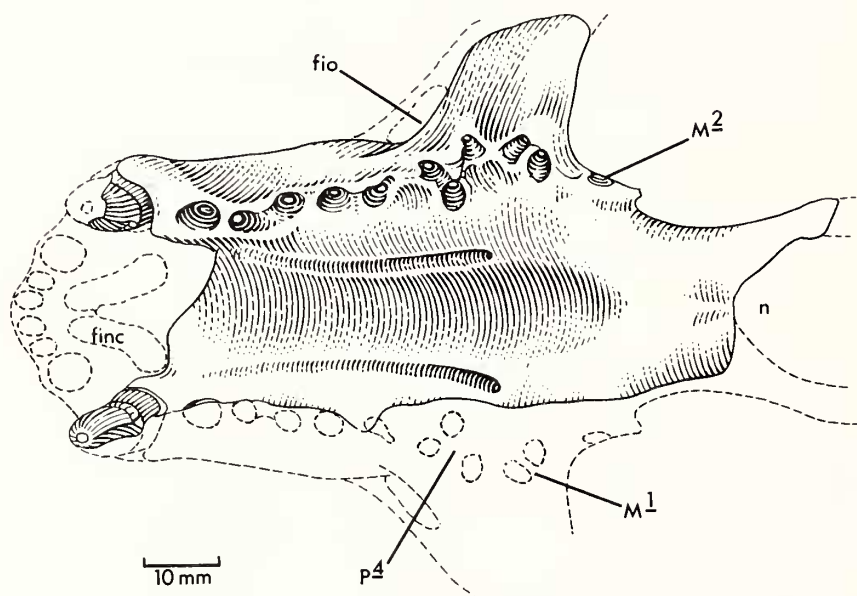


FIGURE 5. *Enaliarctos mitchelli*, new species, paratype, palate with canines, UCMP 80943 from UCMP locality V6618, ventral view with rostral extremity restored from holotype, UCMP 100391, natural size. Abbreviations: finc — incisive foramen; fio — anterior end of infraorbital foramen; n — posterior narial opening; P⁴, M¹, M² — alveoli for fourth upper premolar and first and second upper molars, respectively.

TABLE 1

Differences between *Enaliarctos mealsi* Mitchell and Tedford 1973 and *Enaliarctos mitchelli* new species.

<i>Enaliarctos mealsi</i>	<i>Enaliarctos mitchelli</i>
1. Four posterior palatine foramina on each side of palate.	1. One foramen on each side of palate.
2. Ventral surface of zygomatic arch beneath infraorbital foramen is inclined antero-dorsally and lacks fossa.	2. Surface more horizontal, with fossa
3. Anterior narial opening wide and low, nearly oval in anterior view.	3. Anterior narial opening higher, nearly circular in anterior view.
4. Lateral (cheek) surface of maxilla strongly convex.	4. Lateral surface more vertical, less convex.
5. Posterior border of zygomatic arch joins palate opposite middle of M ¹ .	5. Posterior border joins palate opposite space between M ¹ and M ² .
6. Rostrum flattened dorsoventrally.	6. Rostrum arched dorsoventrally.
7. Posterolabial root of P ⁴ widely separated from the other two roots.	7. Three roots of P ⁴ nearly equidistant and forming nearly equilateral triangle.
8. Nasal bones slope anteroventrally.	8. Nasal bones not sloping, nearly horizontal.
9. Zygomatic arch has continuous dorsal curvature in lateral view.	9. Zygomatic arch flatter, not curved dorsally as much as in <i>E. mealsi</i> .

fossa on the palate between P⁴ and M¹ to receive the crown of the lower carnassial, a posteriorly projecting palatine process, and a constricted posterior palatal extension surrounding the posterior nares. An upper carnassial is inferred but not proven to exist in *E. mitchelli*. As in *E. mealsi*, the palate narrows anteriorly and is transversely arched between the cheek tooth rows. Both species have a median eminence at the posterior end of the palate directly anterior to the posterior narial opening.

The holotype of *E. mealsi* has four posterior palatine foramina on each side of the palate (see Mitchell and Tedford 1973:figs. 5a, 17c). In that species the anterior-most foramen on each side is the largest. It is located medial to the anterior edge of P⁴ and is continuous with an elongate, anteriorly directed palatine sulcus. On both specimens of *E. mitchelli*, there are no smaller posterior palatine foramina; only the one large one (Fig. 5) on each side of the palate that is supposedly homologous with the anterior-most foramen in *E. mealsi*. On both specimens of *E. mitchelli*, the foramina are located farther posterior, being medial to the anterior edge of M¹. There is, obviously, no way to test the significance of this difference in position, but it is consistent in both specimens of *E. mitchelli*. As in *E. mealsi*, each foramen in *E. mitchelli* is continuous anteriorly with a palatine sulcus, which is longer and deeper in the paratype of *E. mitchelli* (UCMP 80943) than in the holotype of the species. The sulcus ends medial to P².

The relationships between the ventral parts of the zygomatic arches and the palates differ between the two species of *Enaliarctos*. On both specimens of *E. mitchelli*, the ventral surface of the zygomatic portion of the maxilla ventral to the infraorbital foramen is more nearly in the same plane as the palate than in *E. mealsi*. Also the ventral surface of the zygomatic arch does not rise dorsolaterally from the side of the skull at such a steep angle as in *E. mealsi*. Lateral to the space between P⁴ and M¹ in *E.*

mitchelli, there is a fossa on the ventral side of the zygomatic arch. This fossa is adjacent to the cheek tooth row. In *E. mealsi* there is no such fossa, and on both known skulls of that species, the uninterrupted ventral surface of the zygomatic arch rises abruptly anterodorsally toward the ventral lip of the infraorbital foramen.

Although no cheek teeth are known for *E. mitchelli*, most of the alveoli for the cheek teeth of both known specimens are in the same positions as on both specimens of *E. mealsi*. The left cheek tooth row on the paratype (UCMP 80943) contains well-preserved alveoli for P¹⁻⁴ and M¹⁻². The following description is based on both that specimen and the holotype (UCMP 100391). The alveolus for P¹ is 2 mm posterior to the canine alveolus, procumbent, and about 4 mm in diameter. P¹ had a single large, round root. P²⁻³ each had two roots aligned in the anteroposterior axis of the cheek tooth row. The two widely diverging roots of P² span approximately 10 mm across their maximum anteroposterior dimension. The anterior root was longer than the posterior one. The two roots of P³ were similarly spread, but on this tooth the posterior root was the longer of the two. P⁴ had three roots, of which the labial two are in the anteroposterior axis of the cheek tooth row. The medial or protocone root of this tooth on the paratype (UCMP 80943) is larger than the two labial roots and is oval-shaped, being expanded in a transverse plane. The three roots of P⁴ on the holotype (UCMP 100391) are of nearly equal size.

There are major differences between the two species of *Enaliarctos* in the positions of roots of P⁴. Compared with both specimens of *E. mealsi*, both specimens of *E. mitchelli* have the three roots of P⁴ relatively closer together and their alveoli are arranged on the palate in a more nearly equilateral triangle (compare Figs. 20a and 20b). This is due to the slightly more posterior

position of the medial or protocone root, and a more antero-medial position of the posterior or talon root in *E. mitchelli*. The striking differences in the P^4 roots of the two species are very evident when the isolated P^4 (LACM 4364) referred to *E. mealsi* is compared with the alveoli of either specimen of *E. mitchelli*. It may be implied from the positions of the alveoli for the roots, that the P^4 in *E. mitchelli*, in comparison with that in *E. mealsi*, had a crown that was relatively smaller, more triangular in occlusal view, and probably less like a carnassial.

In *E. mitchelli*, the posterior labial root of P^4 and the anterior root of M^1 are not positioned as far laterally upon the base of the zygomatic arch as in *E. mealsi* (see Fig. 20). The more medial location of these labial alveoli demonstrates that in *E. mitchelli* the tooth row was in a straighter line than in *E. mealsi*. Modern otariinae have nearly straight cheek tooth rows, and the approach toward this condition in *E. mitchelli* indicates an apparent increase in aquatic adaptation.

In *E. mitchelli*, M^1 had two roots, the posterior one of which was located lingual to the anteroposterior axis of the cheek tooth row. The posterior root was bilobed as shown by the shape of its alveolus, and was probably formed by the fusion of the originally separate lingual and posterior labial roots. The separate, anterior labial root was circular in cross section. The shapes and evolutionary origin of the roots of M^1 are presumably the same as described in preceding text for *E. mealsi*.

M^2 was apparently very small and had a single, bilobed root measuring only 4 mm by 2 mm. It was located at the margin of the palate near the posterior palatine process.

Parts of both canines are preserved on the paratype of *E. mitchelli* (UCMP 80943), and between these two teeth only the proximal anterior part of the crown is not represented. The canine is relatively small, slightly compressed transversely, and has a somewhat recurved conical crown. The complete tip of the right canine is preserved and it is conical with a flat wear facet at its apex. On the posterior side of the crown a vertical crest extends from near the apex proximally to meet the cingulum. The cingulum extends anteriorly to the middle part of the lingual side of the crown. At that point the cingulum ends and merges with another vertical crest that extends half way toward the apex on the lingual side of the crown. On the anteromedial side of the right canine, and interrupted by a break, is a slight vestige of a wear facet that was caused by occlusion with the lower canine. The enamel is smooth and is relatively thin. The overall structure of these canines of *E. mitchelli* is similar to canines of modern Otariinae, especially *Zalophus californianus* (Lesson 1828), but differs from canines of *Allodesmus* spp. which have procumbent, conical crowns that lack vertical crests and have thick, finely rugose enamel.

Enaliarctos sp.

Figures 2 r-s

REFERRED SPECIMENS: LACM 30540, crown of right upper canine collected by E.D. Mitchell, J.H. Lipps, and H. Meals, 26 February 1961; LACM 72381, incomplete crown of right upper canine collected by E.D. Mitchell, 1961 or 1962; both from LACM locality 1626, a locality west of Pyramid Hill correlated with the "grit zone" on the south face of Pyramid Hill.

DESCRIPTION: These two fragmentary canines represent a large (LACM 72381) and a small (LACM 30540) individual. Both are similar in morphology and both are from the same local-

ity (LACM 1626 = UCMP locality V7032) that produced the isolated cheek teeth referred to *Enaliarctos mealsi* in the present paper, and by Mitchell and Tedford (1973). This locality was correlated by Mitchell and Tedford (1973:Fig. 2) with the lower fossil-bearing bed in the "grit zone" on the south face of Pyramid Hill, the probable source of the holotype of *E. mealsi*. These two canines may actually belong to *E. mealsi*, but there is no way to prove this with the known fossils. They resemble the canines of the paratype of *Enaliarctos mitchelli*, and for the purposes of the present study I identify them only as *Enaliarctos* sp. I have included their morphology in the restorations of both *E. mealsi* and *E. mitchelli* (Fig. 18a, b). The canines of these two species were probably similar, if not essentially identical.

Both canine crowns resemble those of the paratype (UCMP 80943) of *E. mitchelli* by being conical, slightly recurved, and by having an irregular posterolingual cingulum that extends between the proximal ends of both a posterior and a medial vertical crest. Both canines have a vertically oriented wear facet on the distal anteromedial part of the crown caused by shearing occlusion with the posterior side of the lower canine. The wear facet on the larger canine, LACM 72381, is faint, but that on the smaller canine, LACM 30540, is more extensive and extends entirely through the enamel. The enamel on both of these canines is relatively thin. The enamel surface is nearly smooth with only slight irregularities.

The smaller of these two canines is approximately the size of the upper canines rooted in the palate of the paratype of *E. mitchelli* (see Table 2). These small canines are 20 to 32 percent smaller than the larger canine, LACM 72381. This disparity in canine size reinforces my previous suggestion, based upon cheek teeth referred to *E. mealsi*, that species of *Enaliarctos* may have been sexually size dimorphic.

Pinnarctidion NEW GENUS

DIAGNOSIS OF GENUS: A genus of the subfamily Enaliarctinae differing from *Enaliarctos* by having a skull with narrower interorbital region, larger orbit, larger antorbital processes, external openings of optic foramina located more ventrally and posteriorly, wider and flatter palate, larger infraorbital palatal plate of maxilla, cheek teeth proportionally smaller and more widely spaced, no embrasure pit for M^1 on palate between P^4 and M^1 , protocone shelf of P^4 , smaller and positioned more posteriorly on the tooth, anterolabial corner of M^1 reduced, posterior narial opening wider and lower, strut between palate and braincase deeply concave lateral to pterygoid hamulus, tympanic cavity larger, paroccipital process larger and joined to mastoid process by large paroccipital-mastoid crest, and occipital condyles more widely separated dorsally.

TYPE SPECIES: *Pinnarctidion bishopi*, new species.

ETYMOLOGY: *Pinna*, Latin, fin; *arktos*, Greek, bear; *idion*, Greek diminutive suffix; in reference to the apparent ursid or arctoid affinities of the subfamily to which this genus of small, aquatic carnivores belongs.

Pinnarctidion bishopi NEW SPECIES

Figures 6-15, 17a, 19a, 21a

Enaliarctos mealsi, part. Mitchell and Tedford 1973:229-232, 237-241, figs. 13, 14 (LACM (CIT) 5302, natural endocranial cast).

TABLE 2

Measurements (in mm) of canine tooth crowns of *Enaliarctos mitchelli* new species, and *Enaliarctos* sp. Estimated measurements are indicated by parentheses.

	<i>Enaliarctos mitchelli</i> both sides, possible female UCMP 80943 Paratype	<i>Enaliarctos</i> sp. LACM 30540 possible female	<i>Enaliarctos</i> sp. LACM 72381 possible male
Anteroposterior diameter			
at base of enamel	8.5	8.4	12.4
Transverse diameter			
at base of enamel	7.2	7.1	9.8
Total crown height	(14.2)	16.0	(20.0)

DIAGNOSIS OF SPECIES: Because the genus *Pinnarctidion* only contains one known species, the diagnoses of the genus and of the type species are identical.

HOLOTYPE: UCMP 86334, skull with left P⁴ and M¹, roots of left P³ and M², lacking anterior end of the rostrum, the right zygomatic arch, the right occipital condyle, and fragments of bone from the dorsal surface of the cranium, collected by Richard C. Bishop, November 1968. The specimen was found in a badly weathered nodule, and the natural matrix endocranial cast was free. The natural endocranial cast was molded and plaster reproductions were made of it, then the nodule was reassembled and I removed the surrounding matrix from the skull. A reproduction of the natural endocranial cast is catalogued under the same number in UCMP with the holotype.

TYPE LOCALITY: UCMP V6916 (= LACM locality 1628). The skull was collected in place from the upper fossiliferous concretion-bearing bed on the south face of Pyramid Hill. The adhering matrix is fine grained and the bone is reddish colored.

REFERRED SPECIMEN: LACM (CIT) 5302, natural endocranial cast with some bone adhering. This specimen was previously referred to *Enaliarctos mealsi* by Mitchell and Tedford (1973). It was collected by the late Dr. Chester Stock in 1950 from CIT locality 481, as a loose specimen on the south face of Pyramid Hill, and its precise stratigraphic source is uncertain. The bone color and adhering matrix are like those of the holotype, and this specimen was possibly derived from the upper bed also.

ETYMOLOGY: The species name honors Mr. Richard C. Bishop. His father, the late Mr. Charles Bishop, Richard Bishop, and his sons, Charles, Patrick, Larry and Steve, three generations of one family, have collected from marine rocks in the vicinity of Bakersfield, California, many important fossils that are now in museum collections.

DESCRIPTION: The holotype skull (UCMP 86334) of *Pinnarctidion bishopi* was found in a weathered nodule that was cracked and partly exfoliated. Pre-depositional weathering of the concretion had removed part of the right side and the rostral extremity. Of the nine suture areas listed by Sivertsen (1954:11)

for age analysis, at least four and probably five exhibit maximum closure. The suture age based on eight preserved sutures of the nine listed, totals a suture age of at least 23, which would classify the animal as an adult, Group I, in Sivertsen's (1954:13) scheme. The presence of at least three open sutures, however, indicates this individual was younger than the ones described previously for *Enaliarctos mealsi* and *Enaliarctos mitchelli*.

The skull of *Pinnarctidion bishopi* is broad and low with a relatively large brain case, small snout, elongate interorbital region, and large orbits. The rostrum is not complete, but its profile in lateral view is not as high as in *E. mitchelli*, and is more like the low profile of *E. mealsi*. The original shape of the anterior narial opening is not discernible due to poor preservation, but appears to have been broad and relatively smaller than in species of *Enaliarctos*. The rostrum is fairly narrow and its sides are not bowed outward as in *Enaliarctos* spp. The nasal bones are almost entirely broken away, and their relationships to the frontals and maxillae are unknown. There are some interdigitating sutures on the top of the rostrum where the maxillae meet the frontals above the anterior edge of the orbit.

There is a nasolabialis fossa on the lateral surface of the rostrum anterior to the orbit as in both *E. mealsi* and *E. mitchelli*. The antorbital process (or lacrimal process) at the posterior edge of this fossa is larger, however, than in both species of *Enaliarctos*. The infraorbital foramen is continuous anteriorly with an elongate, double-grooved fossa dorsal to and paralleling the margin of the cheek tooth row. There is a relatively much smaller fossa in the same position in *Enaliarctos* spp., and it is not divided into two grooves.

The interorbital region of *P. bishopi* is comparatively narrower than in the holotype of *E. mealsi*. Along the midline, the frontals are split by a sagittal fissure that is up to 5 mm deep and extends along the interfrontal suture from the nasal bones to the anterior margin of the brain case. This fissure may be an anomaly or may be an artifact of preservation, but similar, relatively smaller fissures are present on some specimens of modern otariids, particularly adult males of *Otaria byronia* (de Blainville 1820) and females of *Eumetopias jubata* (Schreber 1776). There is a small

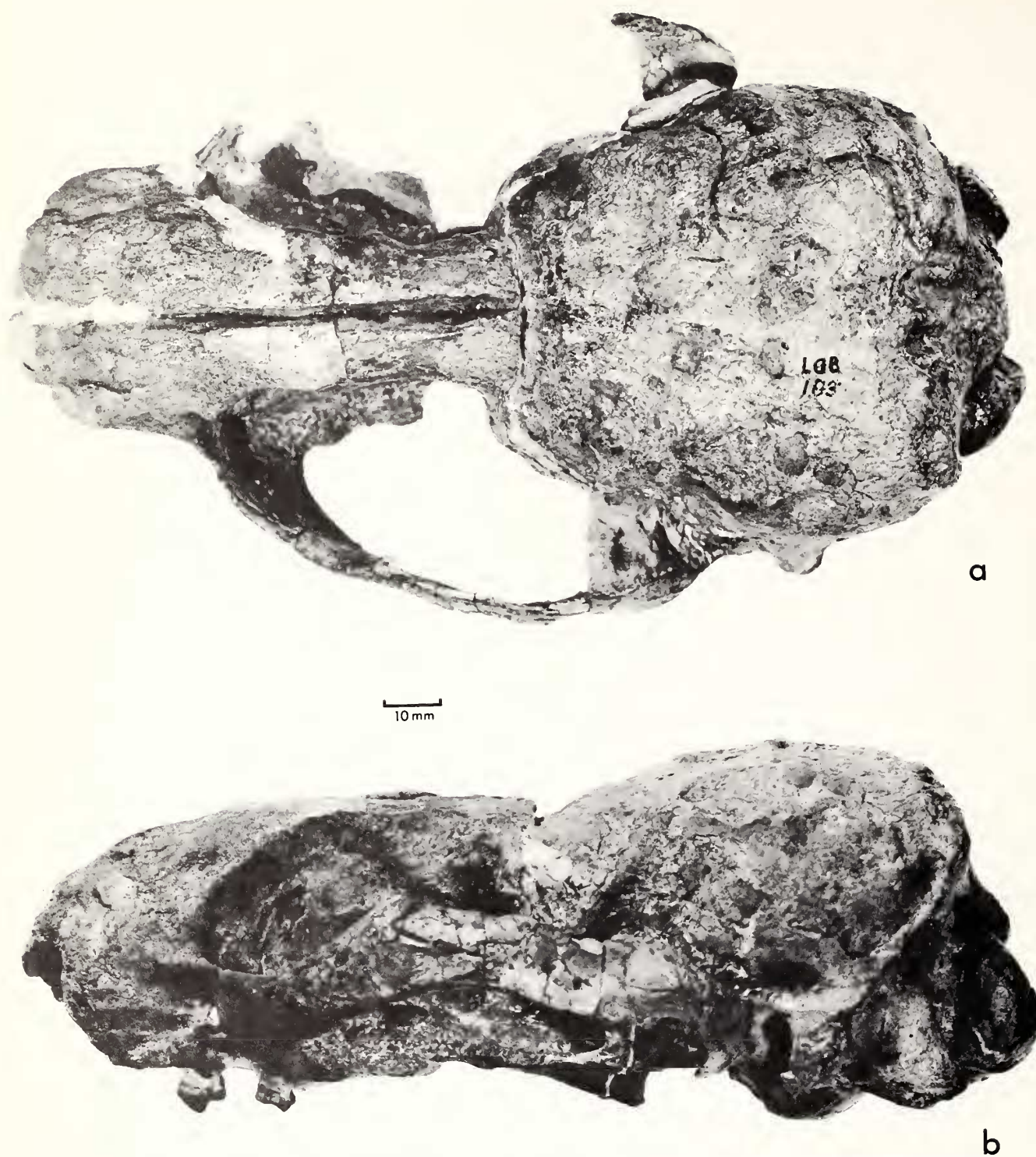


FIGURE 6. *Pinnarctidion bishopi*, new genus and species, holotype, skull with left P⁴ and M¹, UCMP 86334 from UCMP locality V6916, *a*, dorsal view; *b*, left lateral view; natural size.

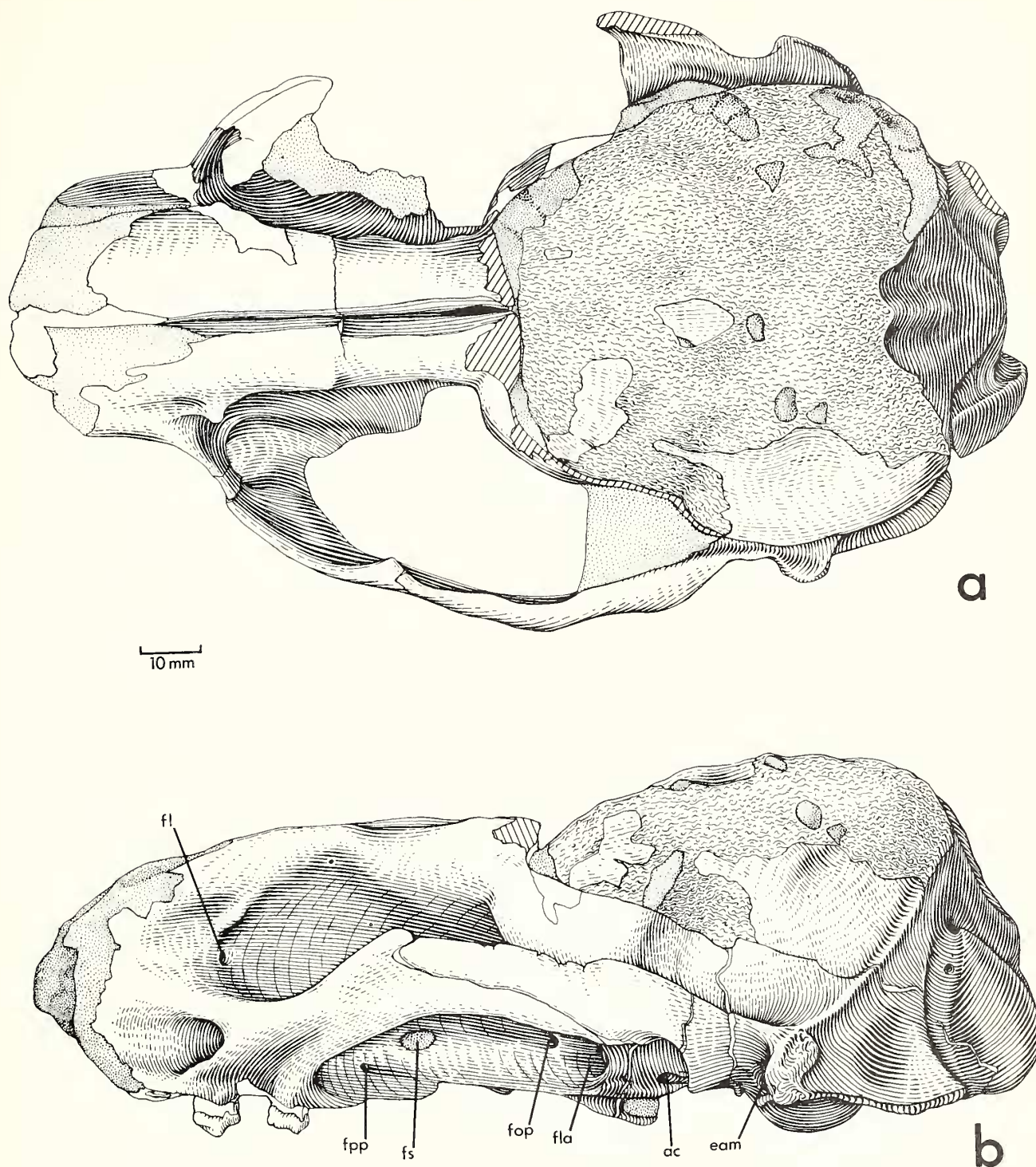


FIGURE 7. *Pinnarctidion bishopi*, new genus and species, holotype, skull with left P⁴ and M¹, UCMP 86334 from UCMP locality V6916; *a*, dorsal view; *b*, left lateral view; natural size. Abbreviations: ac — posterior end of alisphenoid canal; eam — external acoustic meatus; fl — lacrimal foramen; fla — anterior lacerate foramen, anterior end of alisphenoid canal is in the same recess; fop — optic foramen; fpp — posterior end of canal from posterior palatine foramina; fs — sphenopalatine foramen.

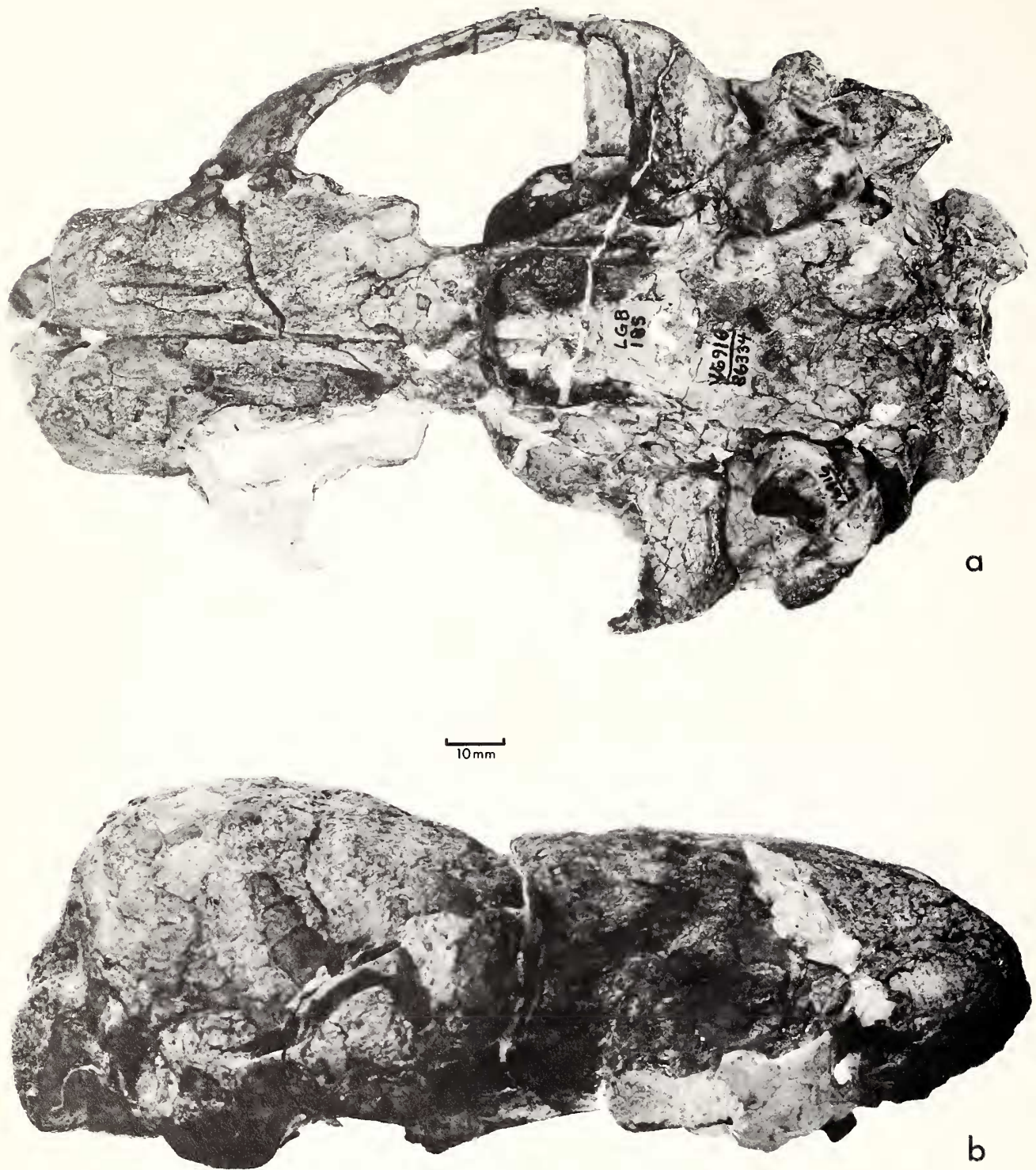


FIGURE 8. *Pinnarctidion bishopi*, new genus and species, holotype, skull with left P⁴ and M¹, UCMP 86334 from UCMP locality V6916; *a*, ventral view; *b*, right lateral view; natural size.

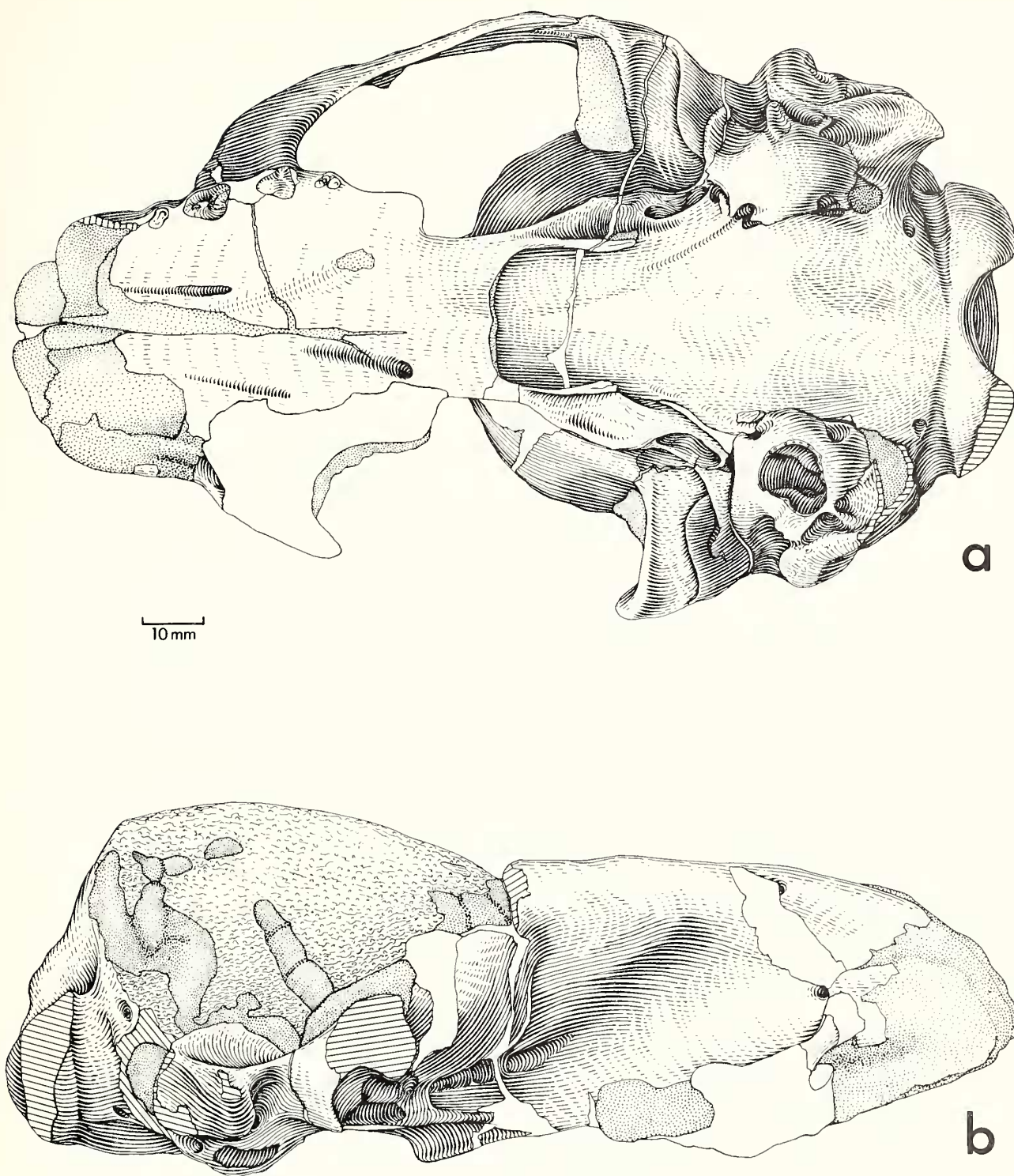


FIGURE 9. *Pinnarctidion bishopi*, new genus and species, holotype, skull with left P⁴ and M¹, UCMP 86334 from UCMP locality V6916; a, ventral view; b, right lateral view; natural size.

supraorbital process, approximately the size of that of *Enaliarctos*, but located relatively farther posteriorly as in *Allodesmus* spp. On the right side of the interorbital region of the holotype of *P. bishopi* there is another small process posterior to the supraorbital process, and this is anterior to a fossa. These are only present on the right side and may be pathologic or anomalous.

The brain case is joined to the interorbital region differently in *E. mealsi* and *P. bishopi*. In *P. bishopi*, a sharper angle is formed by the junction between the interorbital region and the brain case than on the holotype of *E. mealsi*. The brain case of *P. bishopi* is proportionally broader across its anterior part, and the anterolateral corners of the brain case in the temporal fossae are more prominent. In *E. mealsi* the anterolateral corner of the brain case is low within the temporal fossa and the dorsal surface of the interorbital region slopes ventrolaterally toward it. In *P. bishopi* the anterolateral corner of the brain case is relatively higher, being nearly as high as the top of the interorbital region, the surface of which slopes only slightly laterally onto the brain case.

There is no indication of a sagittal crest in *P. bishopi*, but most of the surface of the brain case has been broken off. Along the midline of the brain case, the surface is elevated above the dorsal surface of the interorbital region, the reverse of the condition in *E. mealsi* in which the interorbital region is higher than the brain case. The top of the brain case in *P. bishopi* is irregular and relatively broader than in *E. mealsi*. The surfaces of the parietals in *P. bishopi* follow the contour of the brain and are not raised into a prominent lambdoidal crest as in *E. mealsi*. The supraoccipital is similarly shaped in both species, however it is lower and broader in *P. bishopi*. Both species have a prominent, vertically-oriented fossa on either side of the midline of the supraoccipital below the lambdoidal crest, a prominent strut extending from near the medial side of each condyle to the lamb-

doidal crest, and a deep fossa dorsal to the occipital condyle (Fig. 10). Both species have a prominent medial tuberosity on the supraoccipital at the dorsal margin of the foramen magnum, but this appears smaller in *E. mealsi* because it apparently has been partly chipped away.

In *P. bishopi* the occipital condyles are proportionally more widely spaced and are more divergent dorsally than in *E. mealsi*, in which the medial margins of the condyles are nearly parallel. With the present fossil sample, it is impossible to know whether these differences in the orientation of the condyles have taxonomic significance or represent individual variation as I have suggested (Barnes 1972) is the case in *Allodesmus kernensis*. The condyloid foramina of *P. bishopi* are in about the same location as in the holotype of *E. mealsi*, but are bilaterally asymmetrical. The right condyloid foramen is approximately 2.4 mm wide by 4.5 mm high. The left condyloid foramen is recessed more deeply within the foramen magnum, and is only about 1.5 mm in diameter. In *P. bishopi*, the intercondyloid incisure is approximately as wide as in *E. mealsi*, but is not as deep. In conformity with this shallower incisure, the articular surfaces on the condyles of *P. bishopi* do not curve as far anteriorly on their ventral and lateral sides as in *E. mealsi*. The condyles of *P. bishopi* do not project as far from the occipital shield as in *E. mealsi*, but are more distinctly demarcated ventrally from the basioccipital by a straight transverse sulcus (see Fig. 9a).

The surface of the exoccipital flares anteriorly and ventrolaterally toward the mastoid process (Fig. 7b) in a manner typical of modern Otariinae. The paroccipital process, however, is relatively larger than in otarine species, and is connected to the mastoid process via a large, flattened, paroccipital-mastoid crest. In contrast, the paroccipital process of *E. mealsi* is a small tuberosity and is joined to the mastoid process by only a low, rounded

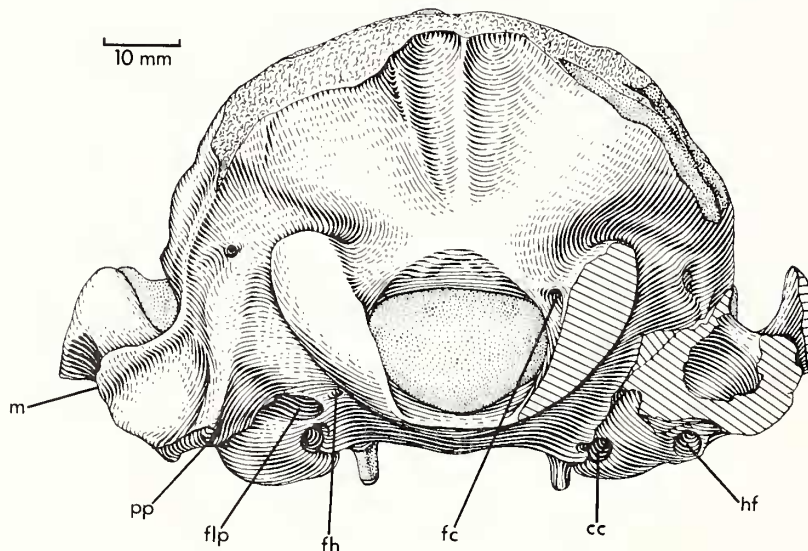


FIGURE 10. *Pinnarctidion bishopi*, new genus and species, holotype, skull, UCMP 86334 from UCMP locality V6916, posterior view, natural size. Abbreviations: cc — posterior carotid foramen; fc — condyloid foramen; fh — hypoglossal foramen; flp — posterior lacerate foramen; hf — tympanohyal pit; m — mastoid process; pp — paroccipital process.

crest. The lateral extension of the paroccipital-mastoid crest of *P. bishopi* enhances the large fossa dorsal to it in the lateral part of the exoccipital. The posterior-most margin of the paroccipital process is directed posteriorly and ventrolaterally, and is separated from the occipital condyle by a wide gap. Because the sutures are fused, it is not known in what proportion the squamosal and exoccipital bones contribute to the formation of the paroccipital process.

The entire structure of the paroccipital-mastoid crest is similar to, but proportionally larger than, the same structure in the modern California sea lion, *Zalophus californianus*, and in the fossil fur seal, *Thalassoleon mexicanus* Repenning and Tedford 1977. In *Allodesmus kernensis* both the paroccipital and mastoid processes are large, however, the crest connecting them is small.

The zygomatic arch of *P. bishopi* is positioned relatively closer to the skull than in *E. mealsi*, and in this respect more closely resembles the condition in *E. mitchelli*, as far as preserved in known specimens (compare Figs. 16a, b, and 17a). In *P. bishopi* the temporal fossa is more constricted posteriorly. This is partly because the brain case is more expanded laterally, and partly because the zygomatic arch does not curve so widely away from the skull, compared with *E. mealsi*. The zygomatic arch of *P. bishopi* is also lower on the skull and does not arch so high at midpoint, resembling *E. mitchelli*. The differences in the shape of the zygomatic arch are associated with the more lateral orientation of the orbit in *P. bishopi* than in *E. mealsi*.

The anterior part of the zygomatic arch that is dorsal to the infraorbital foramen is narrower and more vertically inclined than in either species of *Enaliarctos*. It is neither flared outward as in modern Otariinae, nor retracted and rounded as in *Allodesmus* spp. The anterior surface of the postorbital process of the jugal is inclined at approximately the same angle as in both species of *Enaliarctos*, but the process is relatively more expanded antero-posteriorly. The jugal extends posteriorly ventral to the squamosal as a thin, but relatively dorsoventrally deep process that reaches the anterolateral corner of the glenoid fossa.

The anterior end of the zygomatic process of the squamosal is unique among otariids in its shape and in its relationships with the jugal (see Fig. 7b). In *Enaliarctos* spp. and in species of Otariinae, as in fissiped carnivores, the part of the zygomatic process of the squamosal that is in contact with the jugal tapers anteriorly to a sharp point, and in nearly all individuals and taxa the squamosal does not touch the postorbital process of the jugal. In *P. bishopi*, the squamosal does not taper anteriorly, but ends in a blunt, vertically expanded tip. It not only touches the postorbital process of the jugal, but fits into the notch on its posterior side. This type of articulation was called "mortised" by Mitchell (1968:table V), and is more greatly developed in *Allodesmus* spp. and to a slightly lesser degree in species of Phocidae in which both the postorbital process of the jugal and the zygomatic process of the squamosal are more expanded dorsoventrally.

The margins of the round orbit form a circle approximately 37 mm in diameter. An antorbital (or lacrimal) process is at the anterior edge of the orbit. This process is not as broad-based as the same process in *Enaliarctos* spp., but protrudes farther from the side of the skull. Between this process and the dorsal surface of the zygomatic arch is a broad gap (not a lacrimal fossa) in the otherwise sharply defined border of the orbit. At this gap, the lateral surface of the rostrum is nearly continuous with the medial wall of the orbit. *E. mealsi* differs by having a well defined orbital crest marking this edge of the orbit. In *P. bishopi*, the

opening of the lacrimal canal is approximately 2 mm in diameter, and is located just within the margin of the orbit below the antorbital process.

The lateral extension of the palate is a much flatter and more extensive shelf beneath the orbit and posterior to the infraorbital foramen than in *Enaliarctos* spp. The ventral surface of the orbital opening of the infraorbital foramen is wide and nearly flat.

The medial wall of the orbit is flatter but more recessed than in *Enaliarctos* spp. The opposite walls of both orbits are more parallel than in *Enaliarctos* spp. and converge as closely as 6 mm apart posteriorly. On each side of the holotype of *P. bishopi*, there is a small perforation about 7 mm in diameter in the medial wall of the orbit. This may be homologous with the large orbital vacuities that are characteristic of more modern pinnipeds. Below this perforation and extending posteriorly from the dorsal margin of the infraorbital foramen is a prominent ridge. This ridge marks the medial margin of the infraorbital shelf of the maxilla, and is more prominent and more horizontal than a similar ridge in *E. mealsi* (see Mitchell and Tedford, 1973:222). Below this ridge in *P. bishopi* is the posterior opening of the posterior palatine foramen which is 2 mm in diameter. The foramen enters the bone in an anterior direction. Posterodorsal to this, at the posterior end of the ridge, is the exceptionally large sphenopalatine foramen. The left sphenopalatine foramen measures 7 mm wide and 4 mm high (see Fig. 17b).

The medial wall of the orbit abruptly meets the nearly vertical anterior wall of the brain case. The oblique crest in the postero-dorsal part of the orbital region that merges with the brain case is more prominent and more dorsally located than on the holotype of *E. mealsi*. There is an ethmoidal foramen below the posterior part of this crest in approximately the same location as in *E. mealsi*. The palate is wide and nearly flat, being arched neither anteroposteriorly nor transversely as much as in *Enaliarctos* spp. Compared with *E. mealsi*, the bony palate extends as far posteriorly relative to the anterior wall of the brain case, but is relatively wider and flatter posteriorly. In the place of the small posterior palatine processes of both species of *Enaliarctos*, *P. bishopi* has a wide, thin, squared posterolaterally projecting shelf of the palate beneath each orbit.

The posterior palatine foramina and their associated palatine sulci are more randomly positioned and variably developed than in either known species of *Enaliarctos*, and in this respect *P. bishopi* resembles *Allodesmus packardii*. On the left side of the palate of *P. bishopi*, the largest posterior palatine foramen is located medial to P⁴, slightly posterior to the location of such a foramen in *E. mealsi*, and a deep sulcus extends anteriorly from it. Posterior to this, medial to M², there are at least two sulci that may be associated with smaller foramina, but incomplete preservation of the palate there obscures the evidence. On the right side of the skull of *P. bishopi* there are two much larger foramina associated with sulci. One is medial to M² and the other is farther posterior.

Compared with the deep embrasure pit in species of *Enaliarctos* for the crown of M₁ in the palate between P⁴ and M¹, there is only a slight cavity in *P. bishopi*. This implies a reduced carnassial function of the lower teeth. The palate bears a small median tuberosity at its posterior margin, and this projects slightly posteriorly beneath the internal narial opening. The palatal or ventral margin of the internal narial opening is wider and less curved than in *Enaliarctos* spp. The ventral part of the

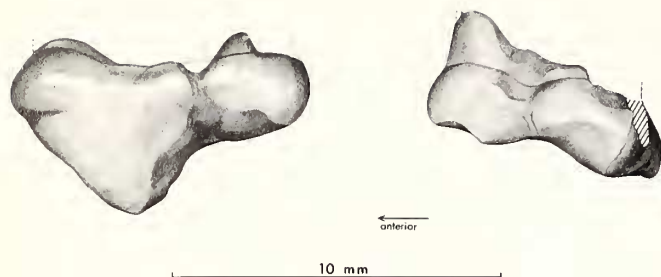


FIGURE 11. *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334 from UCMP locality V6916, left P⁴ and M¹, labial view, slightly larger than 4 x natural size.

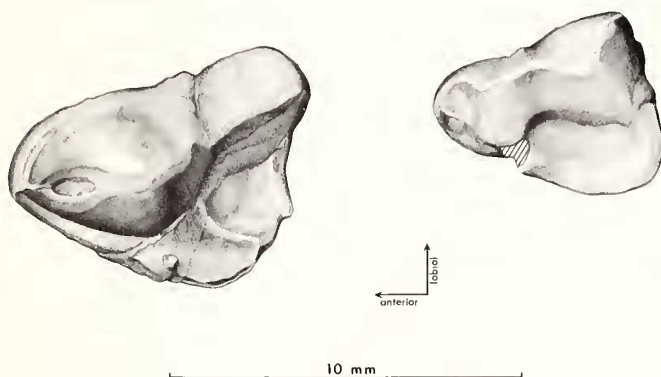


FIGURE 12. *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334 from UCMP locality V6916, left P⁴ and M¹, occlusal view, slightly smaller than 5 x natural size.

zygomatic arch attaches to the rostrum spanning between the anterior root of P⁴ and the space between M¹ and M² (see Fig. 9a). The zygomatic arch of *E. mitchelli* attaches in essentially the same location. In *E. mealsi*, however, the zygomatic arch attaches to the skull relatively farther anteriorly so that its posterior margin is opposite the middle of M¹ (see Fig. 20a).

The dentition of *P. bishopi* is incompletely known. On the holotype, the crowns of P⁴ and M¹ and the roots of P³ and M² are preserved. P³ has a round anterior root which is separated by 3 mm of bone from a bilobed posterior root. The posterior root is bilobed presumably because it was formed by the union of two roots that were once separate. P⁴ apparently has three roots, but they have suffered damage. These three roots are more tightly clustered into an equilateral triangle than in either *E. mealsi* or *E. mitchelli*. The crown of P⁴ (Figs. 11, 12) is a nearly equilateral triangle with a lingual protocone shelf that is slightly posterior to the middle of the tooth. By homology with the cusps on the P⁴ of *E. mealsi* (Mitchell and Tedford 1973:241–242), the paracone is the main labial cusp. It is broad and low, and therefore, unlike the paracone of the P⁴ of *E. mealsi*. There is a wear facet on its anterior edge. The metacone is short and broad and apparently had little shearing capability. It has a lingual wear facet. There is a broad basin lingual to the metacone. A cingulum extends from the anterolingual side of the tooth to the anterolabial side. There

is a small cingular cusp in the middle of the lingual side of the tooth. There is a minimum space of 4.7 mm between the crowns of P⁴ and M¹. This contrasts with *E. mealsi*, in which these two teeth touch (compare Figs. 20a and 21a).

The crown of M¹ is triangular, and shaped somewhat like that of *E. mealsi*, but has lower cusps (Figs. 11, 12). The paracone is lower than the metacone. It is situated on an anterior lobe of the tooth. Compared with the M¹ of *E. mealsi*, the cingulum is less developed, absent labially, and the paracone and metacone are closer to the labial margin of the tooth. As in *E. mealsi* there is a broad posterolingually positioned protocone shelf with a shallow basin, a single anterior root, and a bilobed posterior root with its lingual lobe above the protocone shelf. The anterior alveolus for the M² is 4 mm posterior to the posterior root of M¹, and contains a fragment of a bilobed root. There is another very small posterior root for M². This condition is different from that in *Enaliarctos* spp. in which the M² has one bilobed root.

Each optic foramen is circular and nearly 4 mm in diameter; proportionally and actually larger than in *E. mealsi*. The openings of the optic foramina are located much more ventrally and posteriorly within the interorbital region than in *E. mealsi*. In *E. mealsi*, the external openings of the foramina are just below the mid-part of the brain case. In *P. bishopi* they are recessed beneath the anterior end of the brain case in virtually the same position as in *Allodesmus packardii*. In the past, I have discussed (Barnes 1972:19, 50–51, 62) the unique posteroventral position of the optic foramina (and other nearby structures) in species of *Allodesmus*. In those species and in *P. bishopi*, the internal narial passage is broad and low, and passes through the interorbital part of the skull in a ventral position. In *E. mealsi* and in modern Otariinae, the internal narial passage is narrower and more highly arched through the interorbital region. The optic foramen in these animals is none-the-less, just above the dorsal wall of the narial passage, but is therefore in a more dorsal location.

The optic foramina of *P. bishopi* emerge from the brain case at the narrowest part of the interorbital septum, and are separated by about 6 mm of bone. The optic chiasm is well within the brain case, and the two nerve canals do not merge near the external openings of the optic foramina as they do in *Allodesmus kernensis* and in Recent Otariinae. The anterior lacerate foramina (= orbital fissures) of *P. bishopi* pierce the brain case lateral to and slightly posterior to each optic foramen (see Fig. 7b).

The foramen rotundum of *P. bishopi* lies within the anterior aperture of the alisphenoid canal. This relationship is typical of ursids and canids, but differs from modern Otariinae and Odobeninae in which the foramen rotundum is combined with the anterior lacerate foramen. The greatly enlarged common aperture of the alisphenoid canal and the foramen rotundum in *P. bishopi* is located within a lateral eminence of the pterygoid, and is separated medially from the anterior lacerate foramen by a vertical septum. In *E. mealsi*, the lateral part of the pterygoid is thicker and constricts the anterior aperture of the alisphenoid canal, and the foramen rotundum is merged with the anterior lacerate foramen approaching the condition in modern Otariinae and Odobeninae.

The glenoid fossa of the squamosal in anteroposterior cross section forms a semicircle of approximately 180°. There are both a preglenoid and postglenoid process, but neither is as large as in *E. mealsi*. The preglenoid process is widest toward the lateral margin of the glenoid fossa. The postglenoid process is largest at a more medial location in front of the auditory bulla. The

posterolateral corner of the glenoid fossa is rounded as in *E. mealsi*, and is very different from the prominent corner that is present in *Allodesmus kernensis*. The posteromedial corner of the glenoid fossa is separated by approximately 6 mm from the lateral edge of the Eustachian canal. This proportionally wide separation also exists in *E. mealsi*, in *Allodesmus packardii*, and in some fissiped carnivores, and is unlike what I interpret to be the derived condition in modern Otariinae and in *Allodesmus kernensis* in which the Eustachian canal is much closer to the glenoid fossa (see also Barnes 1972:51–52). Unlike the condition in *E. mealsi*, the posteromedial corner of the glenoid fossa of *P. bishopi* bears a small transverse groove. Both *Allodesmus packardii* and *A. kernensis* have a larger groove in the same location (Barnes 1972:51). The groove leads to a small foramen in the squamosal which may be the canal for the chorda tympani nerve. Medial to this, and separated from it by an eminence in the squamosal as in *Allodesmus packardii*, is the relatively large foramen ovale. It measures 5 mm by 3 mm.

The opening of the posterior nares is ventral to the anterior edge of the brain case (Fig. 9a), and in shape is wide and low, differing greatly from the narrow but high opening in *E. mealsi*. In *P. bishopi* the opening is 23 mm wide and 8 mm high, compared with 24 mm wide and 15 mm high for the holotype of *E. mealsi* (Mitchell and Tedford 1973:223). The roof of the choanal region is nearly flat in *P. bishopi* and this flat surface continues posteriorly beneath the cranium to the basisphenoid surface as one plane. This same surface in *E. mealsi* is much more vaulted both from side to side and from anterior to posterior. At either side of the roof of the choanal region in *P. bishopi* is a pterygoid groove for the palatine (= Vidian) nerve. This groove is absent on the holotype of *E. mealsi* (Mitchell and Tedford 1973:fig. 5a), but is present on the holotype of *Allodesmus packardii* (Barnes 1972:50, figs. 18–19, pl. 1c). The basisphenoid lateral to this groove extends laterally, and in ventral view partly obscures the posterior foramen of the alisphenoid canal and the foramen ovale. In *E. mealsi* these foramina are not so obscured in this view by the basisphenoid. In *P. bishopi*, the entire choanal region, including the bones bordering it, and the posterior narial opening are nearly identical to *Allodesmus packardii*.

The strut formed by the palatine, pterygoid, and alisphenoid bones spanning between the palate and the braincase in *P. bishopi* differs from that of *E. mealsi*. In *E. mealsi*, the strut has a rounded or convex lateral margin extending the total distance from the posterior palatine process to the alisphenoid canal. In its posterior one-half, it bends dorsally toward the brain case. In *P. bishopi* the strut is more slender, and not convex laterally, but has a crest-like lateral margin extending from the palate to the alisphenoid canal (see Fig. 7b, 9a). Lateral to the alisphenoid canal the bone projects laterally in a rugose eminence. A thin ventral crest is continuous with the slender, posteriorly projecting pterygoid hamulus. Between the pterygoid hamulus and the alisphenoid canal, the lateral surface of the bone is excavated into a large fossa. The whole structure in this area in *P. bishopi* is closest to that of *Allodesmus packardii* among the known skulls of fossil and Recent otariids.

In *P. bishopi* the basicranial region between the tympanic bullae is relatively wider than in *E. mealsi*. The pharyngeal tubercle in the center of the basioccipital is nearly as prominent as in *E. mealsi*, but narrower. The posterior lacerate foramen is relatively large. Unlike the shape of this foramen in *E. mealsi*, its transverse dimension (7.3 mm) is greater than its anteroposterior

dimension (6 mm). The shape of this foramen in *P. bishopi* is similar to that in *Allodesmus packardii* and *A. kernensis* (compare Figs. 20a, 21a, and 21b). The openings of the relatively widely spaced hypoglossal foramina face laterally, and they are located directly posterior to the medial edges of the posterior lacerate foramina.

The tympanic bulla (Fig. 13) is relatively more inflated than in *E. mealsi*. The relationship of the bulla to the surrounding bones and structures is similar in *E. mealsi* and other otariid pinnipeds. Judging by a slight ridge and some foramina traversing the surface of the bulla from the area of the anterior carotid foramen to a point lateral to the posterior carotid foramen, the entotympanic forms only a small part of the bulla as in *E. mealsi* and other otariids (see Mitchell and Tedford 1973:254–255; Tedford 1976:fig. 2). As in *E. mealsi*, therefore, the ectotympanic comprises the inflated part of the bulla.

The bulla is fused to the mastoid process and to the postglenoid process. It forms the ventral lip of the external auditory meatus, is notched posteriorly at the posterior lacerate foramen, and is not sutured or fused to the basioccipital. The carotid canal passes almost straight through its medial wall. Compared with *E. mealsi*, the bulla is slightly deeper dorsoventrally in its middle part, and is more inflated in its medial and anterolateral parts. It is not separated from the postglenoid process by as wide a sulcus as in *E. mealsi*, and spreads more extensively over the posterior side of the process. Any remnant of a postglenoid foramen is obscured somewhere within a small transverse crease that marks the contact between the anterior margin of the bulla and the postglenoid process. A postglenoid foramen is present in *E. mealsi* (Mitchell and Tedford 1973:227, with possibly multiple openings on each side), but is characteristically lost in later otariid pinnipeds.

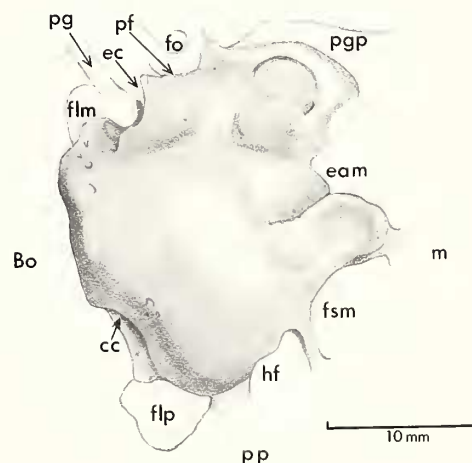


FIGURE 13. *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334 from UCMP locality V6916, left tympanic bulla and adjacent structures, ventral view, 2 x natural size. Abbreviations: Bo — basioccipital; cc — posterior carotid foramen; eam — external acoustic meatus; ec — bony Eustachian canal; flm — median lacerate foramen; flp — posterior lacerate foramen; fo — foramen ovale; fsm — stylomastoid foramen; hf — hyoid fossa; m — mastoid process; pf — petrotympanic fissure; pg — pterygoid groove for palatine (=Vidian) nerve; ppg — postglenoid process of squamosal; pp — paroccipital process.

In previous text I have noted the probable existence in *E. mealsi* of an embayment in the lateral edge of the basioccipital by an inferior petrosal venous sinus. Hunt (1974a, b; 1977) has reviewed the literature and data on the occurrences of such embayments in the lateral edges of the basioccipital in bears and in fossil amphicyonids. In bears the embayment holds an elongate loop of the median branch of the internal carotid artery, and Hunt (1974a:47–48) has suggested that the loop functions as a countercurrent heat exchange mechanism to cool arterial blood in the absence of an orbital rete such as is present in various other carnivores. Hunt (1974b, 1977) has suggested that the embayment in the basioccipital of amphicyonids carried a similar carotid loop.

The evidence for the existence of an embayment in the lateral edge of the basioccipital in *P. bishopi* is as follows: On the holotype of *P. bishopi*, there are small, paired, hemispherical basioccipital tuberosities as in *E. mealsi*. These tuberosities are the probable areas of insertion of the paired rectus capitis ventralis muscles (Miller, Christensen, and Evans 1964:173, 175, fig. 3–29; Howell, 1928:50–51, fig. 4 uses slightly different terminology). As in *E. mealsi*, the tuberosities are ventral to part of the inferior petrosal venous sinuses. On the holotype of *P. bishopi*, the left tuberosity is larger than the right. Where the right petrosal was removed from the skull, an embayment filled with matrix may be seen in the lateral margin of the basioccipital bone. This same matrix-filled embayment in the right side of the

basioccipital may also be seen in the reproduction of the natural matrix endocranial cast of the holotype (see Fig. 15b). On the matrix endocranial cast (LACM [CIT] 5302) referred to the species, the bulla and part of the petrosal had been broken away on the left side and the embayment in the basioccipital is exposed (see Mitchell and Tedford 1973:fig. 13c). Part of the thin ventral wall of the lateral basioccipital tuberosity had broken through, further exposing this embayment. It was partly covered dorsally, within the brain case, by a thin, laterally projecting shelf of the basioccipital that extends to within 3 mm of the medial edge of the petrosal. The embayment widens anteriorly and extends posteriorly as far as the anteromedial edge of the posterior lacerate foramen. This embayment may be homologous with the embayment of the inferior petrosal venous sinus of ursids and amphicyonids and is a character suggesting relationships between them and the Enaliarctinae.

The medial side of the tympanic bulla is nearly vertical and bulges slightly ventral to the lateral margin of the basioccipital. By contrast, in *E. mealsi*, the medial part of the bulla slopes ventrolaterally as a continuation of the plane of the adjacent basioccipital surface. The carotid canal in *P. bishopi* passes nearly straight through the medial side of the bulla. Its posterior foramen encloses a smaller, medially located foramen. The posterior carotid foramen is exposed ventrally because the bulla is retracted anterior to the posterior lacerate foramen. A wide and prominent crest of bone spans between the posterolateral corner of the bulla

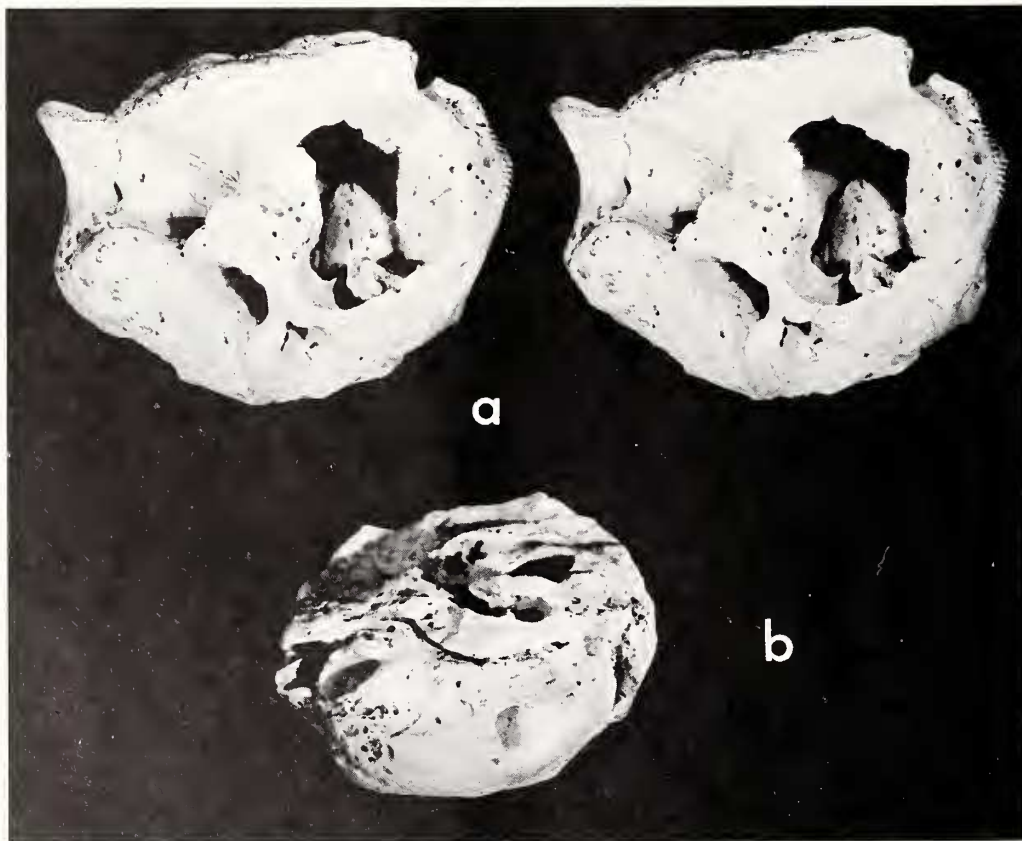


FIGURE 14. *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334 from UCMP locality V6916, right ear region separated from skull, 2 x natural size; a, stereophotographs of ventral view into open middle ear cavity; b, medial side of petrosal and tympanic bulla.

and the ventral side of the paroccipital process. Anterolateral to this crest is the large tympanohyal pit (see Barnes 1972:52, and Mitchell and Tedford 1973:227; the vagina processus styloidei of Mitchell 1968; and Mitchell and Tedford 1973:227, fig. 9). The tympanohyal pit is not obscured by any large projection from the bulla, and faces posterolaterally into a large fossa in the ventral surface of the paroccipital-mastoid crest. This latter fossa is similarly shaped in such Recent Otariinae as *Zalophus californianus* and *Arctocephalus* spp.

A narrow, vertical ridge of bone separates the tympanohyal pit from the stylomastoid foramen. This foramen is directed antero-ventrolaterally, and is compressed between the bulla and the medial side of the mastoid process. Anteromedial to the stylo-mastoid foramen, the ventral surface of the bulla is flat, and extends toward the anteromedial corner of the mastoid process as a horizontal lip that underlies the posterior part of the external auditory meatus. The meatus is nearly circular, approximately 4 mm in diameter, and opens externally in an anterolateral direction. A crest projects laterally from the squamosal above the meatus. A flattened styliform process of the bulla projects anteromedially beneath the anterior opening of the Eustachian canal. Medial to this, however, the bulla is notched ventral to the median lacerate foramen and the anterior carotid foramen.

The tympanic cavity within the bulla is larger than in *E. mealsi*, both relatively and quantitatively. The tympanic cavity is expanded in *P. bishopi* in the same places as in *Allodesmus packardii*. The epitympanic recess is greatly enlarged, being at least twice the size of that in *E. mealsi*, and is expanded antero-laterally. The tympanic crest is relatively large (5 mm in diameter) and projects approximately 4 mm into the tympanic cavity, but is smaller than that of *E. mealsi*. As in *Allodesmus* spp., the ventrolateral wall of the carotid canal creates only a very slight shelf within the cavity in contrast with *E. mealsi*. There is only a vestige of the anterior septum and process which are large in *E. mealsi*, but in the anteromedial corner of the cavity there is a prominent, nearly vertical eminence.

The promontorium of the petrosal is less covered medially by an extension of the bulla than in *E. mealsi*, but is of approximately the same absolute dimensions, making it relatively larger in *P. bishopi*. The fenestra vestibuli faces laterally and is about the same as in *E. mealsi*. There is a groove crossing the antero-medial corner of the promontorium that may have marked the course of the promontory branch of the internal carotid artery. I cannot locate a specific site either of the promontory foramen or of a foramen in the medial wall of the bulla where the promontory branch might have diverged from the median branch of the internal carotid artery. In the expected location of either structure, however, there are two or three possible small holes, one of which could be the structure in question.

There does not appear to be a distinct fossa for the tensor tympani in *P. bishopi* as was described for *E. mealsi* (Mitchell and Tedford 1973:228, fig. 9). Such a fossa is present in fissipeds. The problem in interpreting the structure in the holotype of *P. bishopi* is because the roof of the tympanic cavity lateral to the

promontorium is partly broken away. There is a faint groove leading from the Eustachian canal to this area, but there are no ridges demarcating a fossa as in *E. mealsi*.

The right petrosal and tympanic bulla were found broken from the remainder of the holotype skull of *P. bishopi* when it was discovered in the field. The top of the petrosal is therefore visible. Because of the breakage, however, there are some difficulties in interpreting the relationship between the bony tentorium and the petrosal. My interpretation is that the tentorium contacted the lateral margin of the petrosal, but that this contact, unlike the condition in walruses or ursids, did not extend much toward the opening of the floccular fossa, and that the tentorium projected into the brain case in a more horizontal position than is typical of modern Otariinae. The floccular fossa is relatively very large, having an estimated inside diameter of 7 to 8 mm. The aperture is smaller (4 mm by 5 mm in diameter), and nearly circular. This fossa is much larger than in *Allodesmus kernensis*. The petrosal resembles those of both *Imagotaria downsi* (holotype, SBMNH 342; Mitchell 1968; fig. 7) and *Allodesmus kernensis* (referred specimens, UCMP 81708, 83363; Barnes 1972:6) by being broad, dorsoventrally flattened, and by having a dorsoventrally flattened, bilobed internal acoustic meatus in which the facial nerve canal and the vestibulocochlear nerve canal are separated by low septa. The petrosal apex is incomplete, but it appears from the shape of the petrosal as preserved that the apex is not significantly enlarged (Fig. 14b). In none of these structures is the petrosal of *P. bishopi* remarkably similar to those of modern Otariinae.

The isolated natural matrix endocranial cast, LACM (CIT) 5302, that Mitchell and Tedford (1973:229–232, 237–241, figs. 13, 14) referred to *E. mealsi* is nearly identical in morphology to the endocranial cast (Figs. 15a–b) of the holotype (UCMP 86334) of *P. bishopi*. I reidentify the isolated endocranial cast, LACM (CIT) 5302, as belonging to *P. bishopi* on the basis of the following characters of *P. bishopi* that differ from the holotype (LACM 4321) and the other specimen (LACM [CIT] 5303) confidently referred to *E. mealsi*: The posterior lacerate foramen is larger and expanded transversely rather than anteroposteriorly. The basisphenoid is not arched and is more in the same plane as the basioccipital. The optic foramina are larger in diameter, closer together, and positioned more ventrally and posteriorly beneath the anterior edge of the brain. The anterior lacerate foramen is broader, lower on the brain case, and at least dorsally, bilobed. The fossae on the supraoccipital dorsal to the condyles are deeper and wider. The part of the exoccipital that descends toward the paroccipital process is more expanded reflecting the larger size of that process. The endocranial cavity is proportionally and measurably wider, particularly across the anterolateral corners. Relative to its width, the endocranial cavity is flatter dorso-ventrally. The coronal gyrus and the anterior ectosylvian gyrus are more vertically oriented and enlarged. The enlargement emphasizes the depth of the pseudosylvian sulcus on the endocranial cast, but the sulcus is not expressed by as profound a sulcus on the external wall of the brain case as in *E. mealsi*.

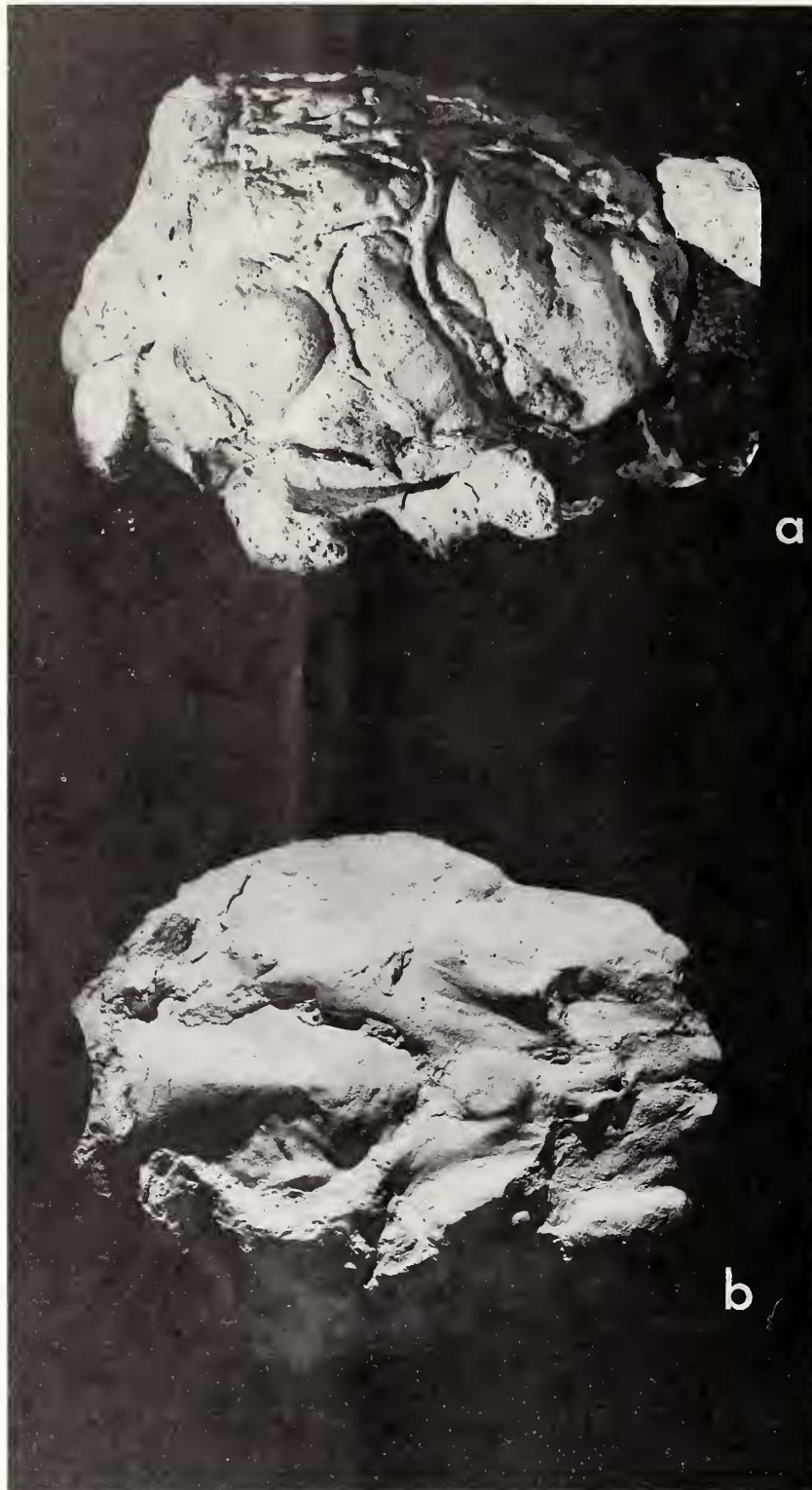


FIGURE 15. *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334 from UCMP locality V6916, natural matrix endocranial cast, natural size; *a*, right lateral view of endocranial cast subsequent to removal of damaged surface bone; *b*, ventral view of reproduction of matrix endocranial cast made prior to reassembly of broken skull.

TABLE 3

Measurements (in mm) of skulls of Enaliarctinae from Pyramid Hill, California. Methods of making measurements were as defined by Sivertsen (1954:18–20, those followed by the number given by Sivertsen for the same measurement) or by Barnes (1972:fig. 1, those followed by a dot). Other measurements are explained in text under *Methods*. Parentheses indicate estimated measurements. Asterisks indicate measurements with values differing from those given by Mitchell and Tedford (1973).

	<i>Enaliarctos mealsi</i> Mitchell and Tedford 1973		<i>Enaliarctos mitchelli</i> new species		<i>Pinnarctidion bishopi</i> new genus and species	
	LACM 4321, holotype	LACM(CIT) 5303, referred	UCMP 100391, holotype	UCMP 80943, paratype	UCMP 86334, holotype	LACM(CIT) 5302, referred
Post-palatal length (palatal notch to basion).....	92.5	—	—	—	80.5	—
Basion to anterior edge of zygomatic root (18)	144.7*	124.7*	—	—	130.2	—
Length of tooth row, C to M ² (●)	—	—	63.0	69.2	—	—
Width of rostrum across canines (12)	—	(43.)	40.9	(42.)	—	—
Width of palate across ante- rior alveoli of P ⁴ (●)	55.0*	48.6*	42.4	(44.)	(44.)	—
Width between infraorbital foramina (●)	53.8	49.7	42.0	(46.)	41.0	—
Width across antorbital processes (5)	(47.0)	(42.)	41.1	—	36.8	—
Width across greatest inter- orbital constriction (6) ...	39.6	32.2	28.1	—	26.1	—
Width across supraorbital processes (7).....	37.6	30.9	26.7	—	26.3	—
Width across greatest inter- temporal constrict- ion (●)	31.0	26.0	19.8	—	21.4	—
Width of braincase at ante- rior edge of glenoid fossa (8)	58.1	(57.)*	—	—	(59.)	(60.)
Zygomatic width (17)	(136.)	—	(106.)	—	(104.)	—
Auditory width (19)	(90.)	—	—	—	82.6	—
Mastoid width (20)	(98.)	—	—	—	90.6	—
Paroccipital width	65.7	—	—	—	(78.)	—
Greatest width across occipital condyles	45.7	—	—	—	49.0	—
Greatest width of anterior nares (●)	—	30.6	30.0	—	—	—
Greatest height of anterior nares	—	(21.0)	26.0	—	—	—
Width of zygomatic root of maxilla (14)	14.3*	13.6*	13.4	15.7	16.6	—
Greatest width of foramen magnum	23.8	(24.5)	—	—	24.1	(25.)
Greatest height of foramen magnum	16.5	(18.4)	—	—	14.7	(19.)
Transverse diameter of infraorbital foramen	10.0	9.5	8.6	(8.5)	7.2	—

DISCUSSION

The present recognition of a total of three species within two genera of primitive otariid pinnipeds of late Oligocene or early Miocene age provides a new perspective on the evolutionary diversity and classification of enaliarctine pinnipeds. The new genus *Pinnarctidion* is similar to *Enaliarctos* in many characters, most of them primitive, but it shares many apparently unique derived characters with the subfamily Allodesminae, to which it is probably ancestral.

The assignment of *Pinnarctidion bishopi* to the otariid subfamily Enaliarctinae and the re-interpretation of the holotype of *Enaliarctos mealsi* eliminates or modifies some of the characters used by Repenning and Tedford (1977:11) to diagnose the family Enaliarctidae. The emended diagnosis of the subfamily presented in previous text reflects this.

The interpretation of subfamily and family level classification of fossil and modern otariid pinnipeds has varied markedly between different authors (see Mitchell 1966, 1968, 1975; Barnes 1972; Repenning 1975, 1976; Repenning and Tedford 1977; Tedford 1976). I believe that the recognition of the four families Enaliarctidae, Desmatophocidae, Odobenidae, and Otariidae (Repenning 1975, 1976; Repenning and Tedford 1977) is unwarranted. Equal consideration of the morphologic characters used by Repenning and Tedford (1977:8–12) to define these families might require the establishment of yet another family group for the new genus *Pinnarctidion*.

I recognize several distinct lineages of otariid pinnipeds and give them subfamily rank. To include *Pinnarctidion bishopi* in the subfamily Enaliarctinae may stretch the concept of that subfamily and make it a horizontal group. As such, however, I recognize the Enaliarctinae as a common ancestral group from which several other derived groups originated (see Repenning 1975:fig. 11; 1976:376–379; Repenning and Tedford 1977:fig. 6). This concept of the relationship of such a group to its derivatives is similar to that which the family Palaeoryctidae is thought to have to several mammalian orders (*sensu* Lillegraven 1969:fig. 40), or which the subfamily Hyracotheriinae is thought to have to other subfamilies of the Equidae.

I believe that some middle ground exists in which the classification of otariid pinnipeds is internally consistent and is comparable to the family level classifications of other mammals. To this end, I employ a classification that includes one family, the Otariidae, with six subfamilies. The subfamily Dusignathinae (Mitchell 1968) I include in the Odobeninae, and the subfamily Desmatophocinae, as previously used by Mitchell (1966) and myself (1972), I now divide into the Desmatophocinae and the Allodesminae following Mitchell's later (1968, 1975) papers. The broad phylogenetic relationships, I believe, are basically as shown by Repenning (1975) and Repenning and Tedford (1977), except in details of the relationships which the Allodesminae and Desmatophocinae have with the Enaliarctinae. These relationships are discussed below following the observations on enaliarctine species.

Enaliarctos remains the most primitive otariid genus yet described. Many of the characters it has that distinguish it from *Pinnarctidion* and from derived otariids are fissiped-like and are interpreted as being primitive. I have described the structure of its foramen rotundum, alisphenoid canal, and anterior lacerate foramen as intermediate between such fissipeds as the canids or ursids and the modern otariines. The zygomatic arch, palate, or-

bit, and basicranium share many characters with fissiped carnivores as noted by Mitchell and Tedford (1973). I also agree with suggestions that *Enaliarctos* is near the ancestry of the Otariinae (Mitchell and Tedford 1973; Mitchell 1975:19–20, fig. 1; Repenning and Tedford 1977:fig. 6).

Of the two currently known species of *Enaliarctos*, the more primitive one, *E. mealsi*, is known by skulls that are probably from the lower concretion-bearing bed in the basal part of the Pyramid Hill Sand Member of the Jewett Sand, and by isolated teeth from a stratigraphically correlative nearby locality. Both the holotype and paratype of the more derived species, *E. mitchelli*, are probably from the higher fossiliferous concretion-bearing bed in the Pyramid Hill Sand Member. Thus, the available evidence suggests that the morphologically more derived species of *Enaliarctos* occurs stratigraphically higher, and is, therefore, geochronologically younger than the more primitive species.

This chronologically younger species, *E. mitchelli*, differs from *E. mealsi* by possessing the following apparently derived characters: high rostrum, larger nares, fewer posterior palatine foramina, zygomatic arches that are not so greatly arched at mid-point, more horizontal ventral surface of the zygomatic arches beneath the infraorbital foramina, relatively narrower interorbital region, straighter cheek tooth row, and roots of P⁴ relatively closer together suggesting at least partial suppression of the carnassial function of this tooth. I believe that these characters are derived for *E. mitchelli* because they either depart from conditions in generalized terrestrial fissipeds, or approach aquatic adaptations in modern pinnipeds, or both. The significance of some other characters in which *E. mitchelli* differs from *E. mealsi* is uncertain. Such characters are the higher rostrum and more anterior position of the roots of M¹ relative to the origin of the zygomatic arch. The heightened rostrum is probably correlated with the enlargement of the anterior narial opening; an aquatic adaptation. The meanings of some of these differences may be understood when other species of enaliarctines are described. It is interesting to note that the high rostrum and large anterior narial opening of *E. mitchelli* resemble those of some Recent phocids, particularly the Weddell seal, *Leptonychotes weddelli* (Lesson 1826) and the Grey seal, *Halichoerus grypus* (Fabricius 1791). In contrast, the narrower rostrum and smaller narial opening of *E. mealsi* bear a closer resemblance to Recent species of the genera *Phoca* Linnaeus 1758 and *Pusa* Scopoli 1777.

Both the taxonomic diversity and some of the morphological characters of various mid-Cenozoic otariids have previously (Mitchell 1968:1887–1888, 1892; 1975; Barnes 1972:63–65) been compared with those of more recent true seals of the family Phocidae. It is becoming apparent that North Pacific otariids were previously more diversified than they are now and may have occupied some of the niches now filled by phocids. It is probably quite significant that even among the earliest fossil otariids, some species had characters that were convergent with phocids.

The third known late Oligocene or early Miocene enaliarctine, *Pinnarctidion bishopi*, differs markedly from species of *Enaliarctos*. The holotype of *P. bishopi* is known to have come from the upper fossiliferous concretion-bearing bed at Pyramid Hill, and was probably at least contemporaneous with, if not sympatric with, *E. mitchelli*. The morphology of the skull of *P. bishopi* suggests that this species had attained a greater degree of aquatic adaptation than either *E. mealsi* or *E. mitchelli*. Most of the char-

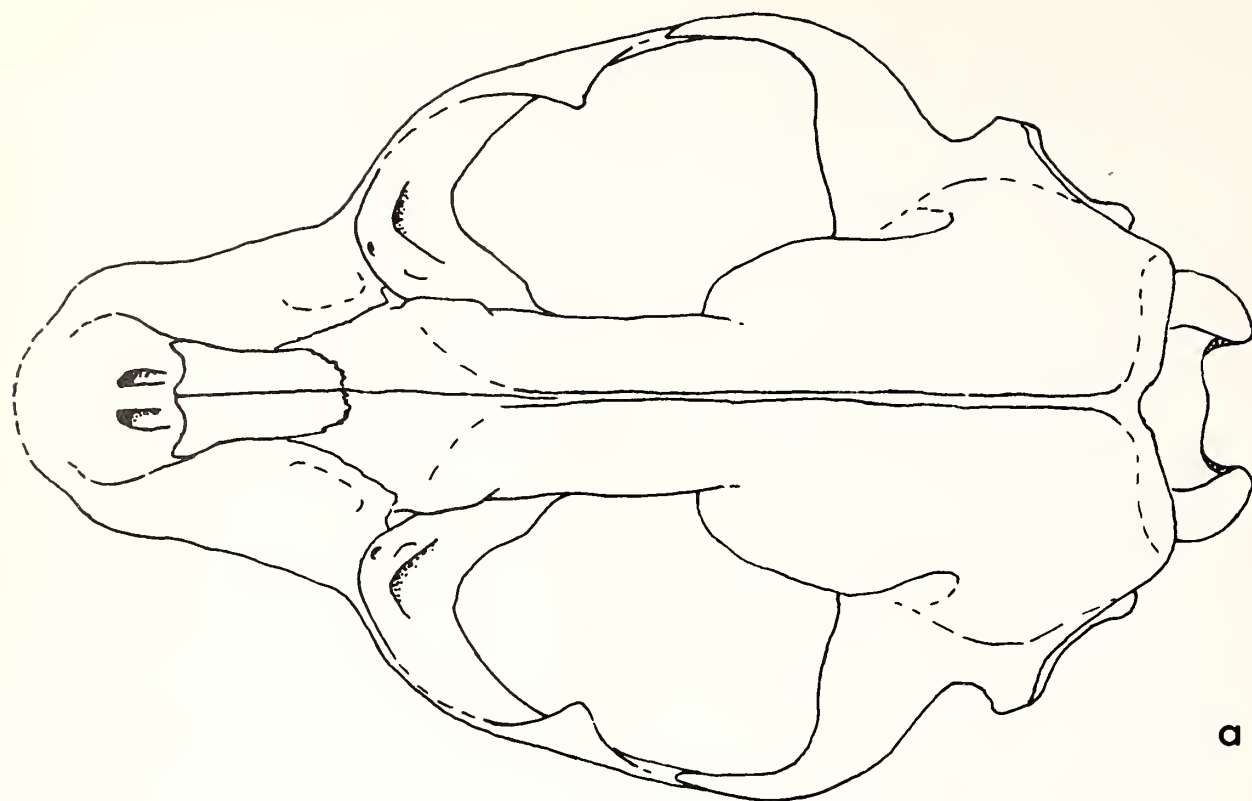
TABLE 4

Characters shared by *Pinnarctidion bishopi* new genus and species, and *Allodesmus packardi* Barnes 1972 or *A. kernensis* Kellogg 1931, that differ from *Enaliarctos* spp. An asterisk denotes characters known in *A. kernensis* and presumed to also exist in *A. packardi* although not preserved.

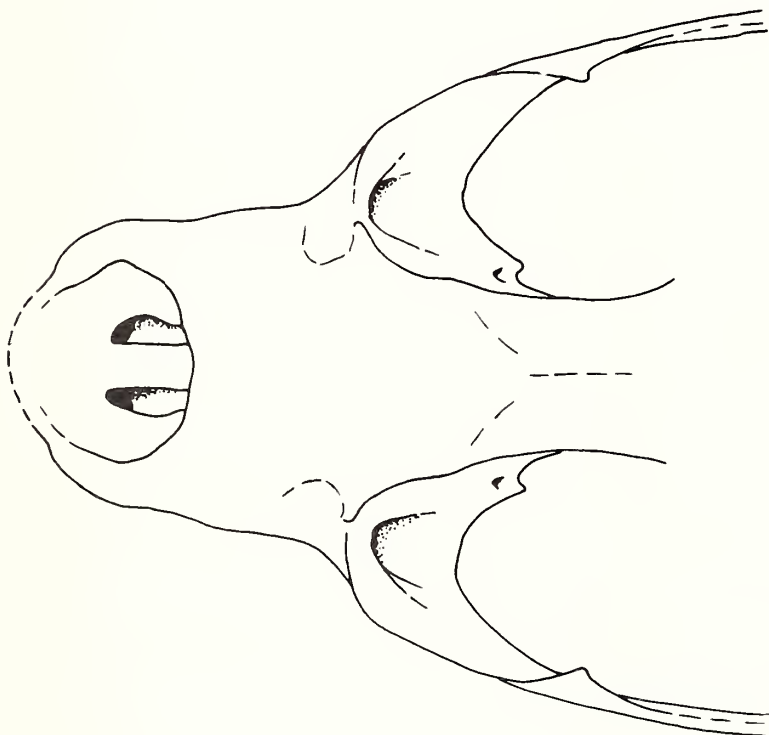
<i>Pinnarctidion bishopi</i> and <i>Allodesmus</i> spp.	<i>Enaliarctos</i> spp.
1. Palate broad and relatively flat.	1. Palate relatively narrower and arched.
2. Pterygoid strut between braincase and palate is excavated laterally.	2. Pterygoid strut is rounded and inflated on lateral surface.
3. Occipital condyles diverging dorsally.*	3. Condyles nearly parallel.
4. Paroccipital process large.*	4. Paroccipital process small.
5. Posterior nares wide and low.	5. Posterior nares relatively narrower and higher.
6. Infraorbital process of palate thin and expanded laterally.	6. Process small and spur-like.
7. Preglenoid process small.	7. Preglenoid process relatively larger.
8. Optic foramen posteroventrally located beneath anterior end of braincase.	8. Foramen anterodorsally located in front of braincase.
9. Dorsal surface of braincase equal to or higher than dorsal surface of interorbital region.	9. Braincase lower than dorsal surface of interorbital region.
10. Anterior lacerate foramen (= orbital fissure) large and bilobed.	10. Foramen relatively smaller and more circular.
11. No sagittal crest on interorbital region.	11. Sagittal crest on interorbital region.
12. Skull flattened dorsoventrally.	12. Skull arched dorsoventrally.
13. Mastoid process cubic.	13. Mastoid process more rounded.
14. Zygomatic arch low and nearly paralleling palatal-basioccipital plane.	14. Zygomatic arch more curved dorsally at midpoint.
15. Palatal margin lateral to posterior part of choanal area sharp edged laterally.	15. Margin smoothly rounded laterally.
16. Fossa in alisphenoid anteromedial to glenoid fossa.	16. Fossa medial to glenoid fossa.
17. Epitympanic recess in ear cavity large.	17. Epitympanic recess small.
18. Cheek teeth with wide spaces between them.	18. Cheek teeth closely spaced.
19. Posterior lacerate foramen elliptical transversely.	19. Foramen elliptical anteroposteriorly.
20. Zygomatic arch joins rostrum near palatal plane.	20. Zygomatic arch descends dorsolaterally from palatal plane.
21. Median lacerate foramen visible in ventral view.	21. Median lacerate foramen covered by anteromedial corner of bulla.
22. Lambdoidal crest low, rounded.	22. Crest more prominent.
23. Sagittal crest small or absent.	23. Sagittal crest prominent.
24. Apex of postorbital process of jugal is expanded anteroposteriorly.	24. Apex is narrow, pointed.
25. Anterior extremity of zygomatic process of squamosal is expanded dorsoventrally and contacts postorbital process of jugal.	25. Anterior extremity pointed, not expanded dorsoventrally, and does not contact postorbital process of jugal.

acters separating it from either species of *Enaliarctos* are derived characters, apparent aquatic adaptations, or characters shared with geochronologically younger species of *Allodesmus*, especially the middle Miocene *Allodesmus packardi*. Table 4 lists 25 characters shared by *P. bishopi* with *A. packardi* and/or *A. kernensis*, and not shared with *Enaliarctos mealsi* and *E. mitchelli*. These numerous similarities, and the fact that *P. bishopi* is chronologically older than any species of *Allodesmus*, suggest that it may be the ancestor of *Allodesmus*. Although *Allodesmus packardi* is more derived in its dental characters than *A. kernensis*,

it is more primitive in its basicranial characters. The following ten characters of *P. bishopi* separate it from *A. packardi*: cheek teeth multiple rooted, orbital vacuity small (or absent?), zygomatic process of the jugal not so greatly expanded dorsoventrally, infraorbital foramen more recessed beneath the flange-like anterior orbital margin of the zygomatic arch, interorbital region relatively wider, presence of the antorbital process, bulla more inflated, tympanic crest wider and extended more into the tympanic cavity, and presence of the nasolabialis fossa. These characters are shared with *Enaliarctos* spp., but are primitive,



a



b

FIGURE 16. Restorations of skulls: a, *Enaliarctos mealsi* Mitchell and Tedford 1973, holotype, LACM 4321, and referred specimen, LACM (CIT)5303; b, *Enaliarctos mitchelli*, new species, holotype, UCMP 100391; both dorsal views reduced to approximately the same cranium length. (a modified from Mitchell and Tedford 1973:fig. 17a, with anterior-most rostral extremity in part from *E. mitchelli*, new species.)

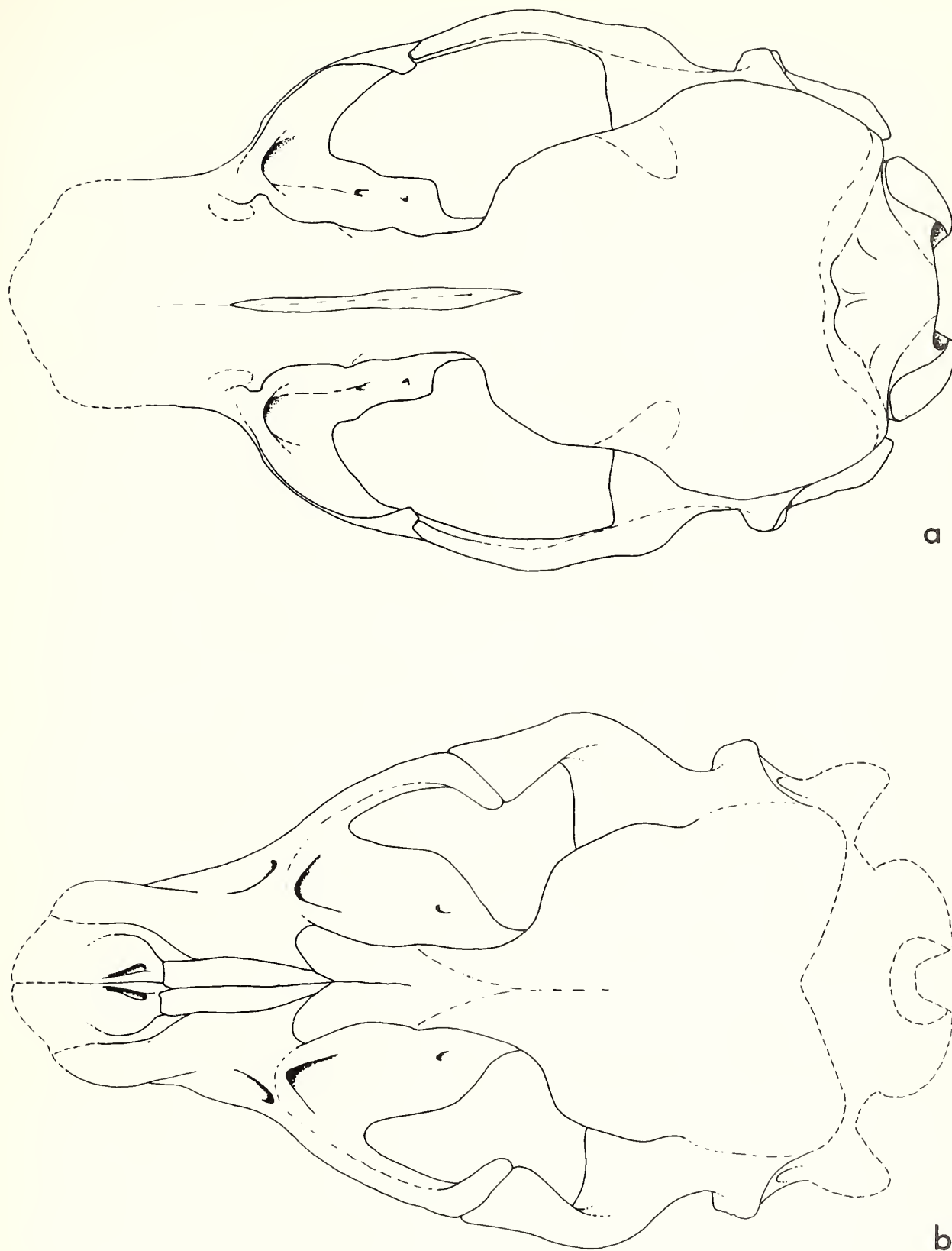


FIGURE 17. Restorations of skulls: *a*, *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334; *b*, *Allodesmus packardi* Barnes 1972, holotype, CAS 4371A; both dorsal views reduced to approximately the same cranium length. (*b* modified from Barnes 1972:fig. 21a.)

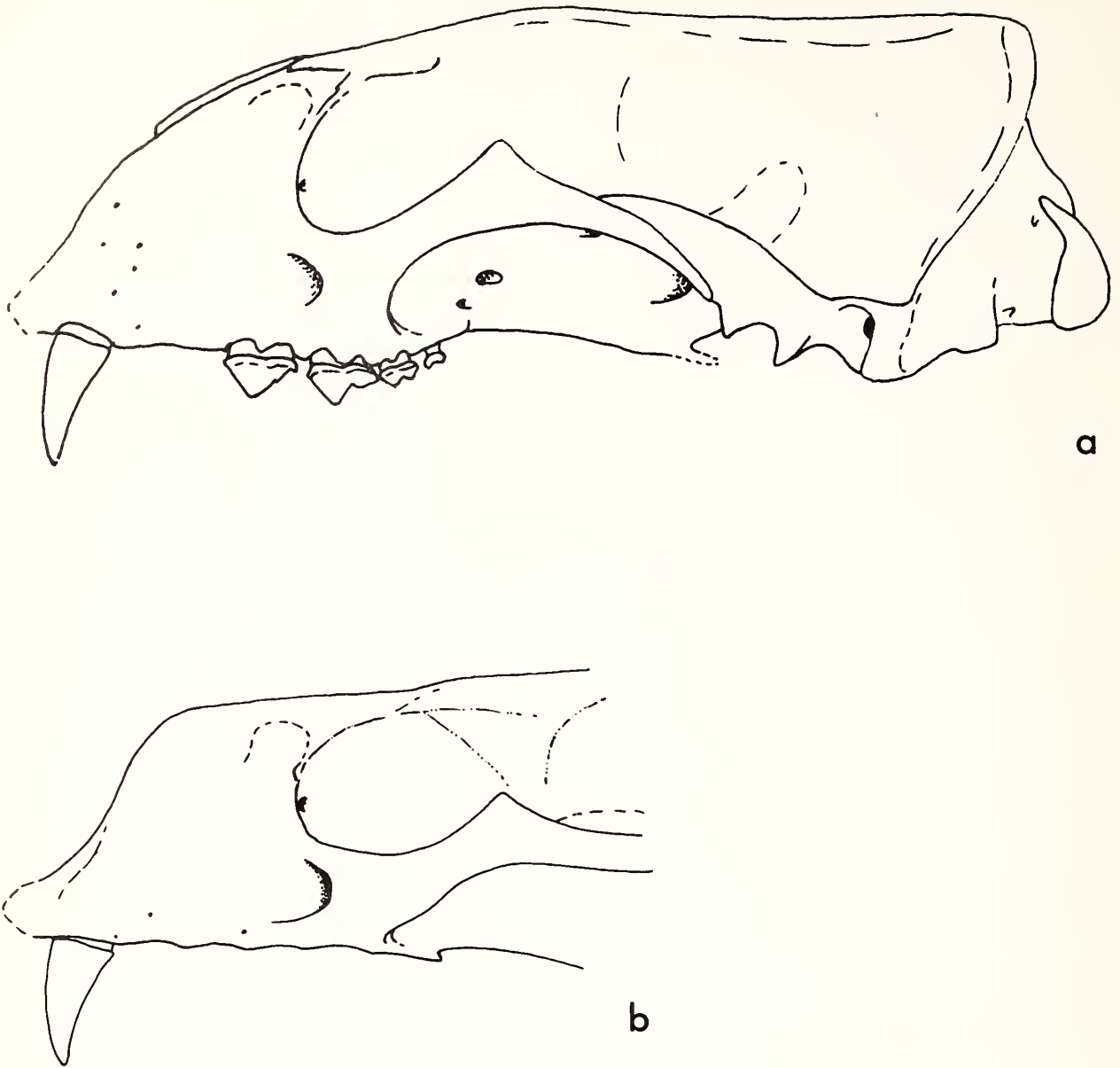


FIGURE 18. Restorations of skulls: *a*, *Enaliarctos mealsi* Mitchell and Tedford 1973, holotype, LACM 4321, and referred specimen, LACM (CIT) 5303; *b*, *Enaliarctos mitchelli*, new species, holotype, UCMP 100391, and paratype, UCMP 80943; both left lateral views reduced to approximately the same cranium length. (*a* modified and reversed from Mitchell and Tedford 1973:figs. 6b, 17b, with anterior-most part of rostrum and canine in part from *E. mitchelli*, new species.)

however, and do not preclude *P. bishopi* from being an ancestor of *A. packardii*. Further modification of some of these structures, particularly in the specializations that are considered aquatic modifications, could lead to the structures present in *A. packardii*.

All known enaliarctines share with *A. packardii* the deep vertical sulcus on the lateral wall of the cranium in the area of the pseudosylvian sulcus of the brain (see Mitchell and Tedford 1973:239). Such a sulcus is minimal to non-existent on the crania of *A. kernensis* and Recent otariids. There are profound differences in the structure of the anterior orbital margin on the zygomatic arch. I have previously described (Barnes 1972:14) the unique retracted dorsal margin of the infraorbital foramen and the

rounded anterior orbital margin in *Allodesmus* spp., and this differs from the more sharp margin in fissiped carnivores, in enaliarctines (including *P. bishopi*), and in modern otariines. This may be a diagnostic character for Allodesminae.

The morphologic similarities and suggested ancestral-descendant relationship between *Pinnarctidion bishopi* and *Allodesmus* spp. probably exclude *Desmatophoca oregonensis* from some intermediate position in the same lineage. *D. oregonensis* has usually been considered to be closely related to *Allodesmus* or to be close to the ancestry of that genus (Mitchell 1966, 1968, 1975; Barnes 1972; Repenning 1975; Repenning and Tedford 1977). Mitchell (1968:1888; 1975:13) suggested that the common ances-

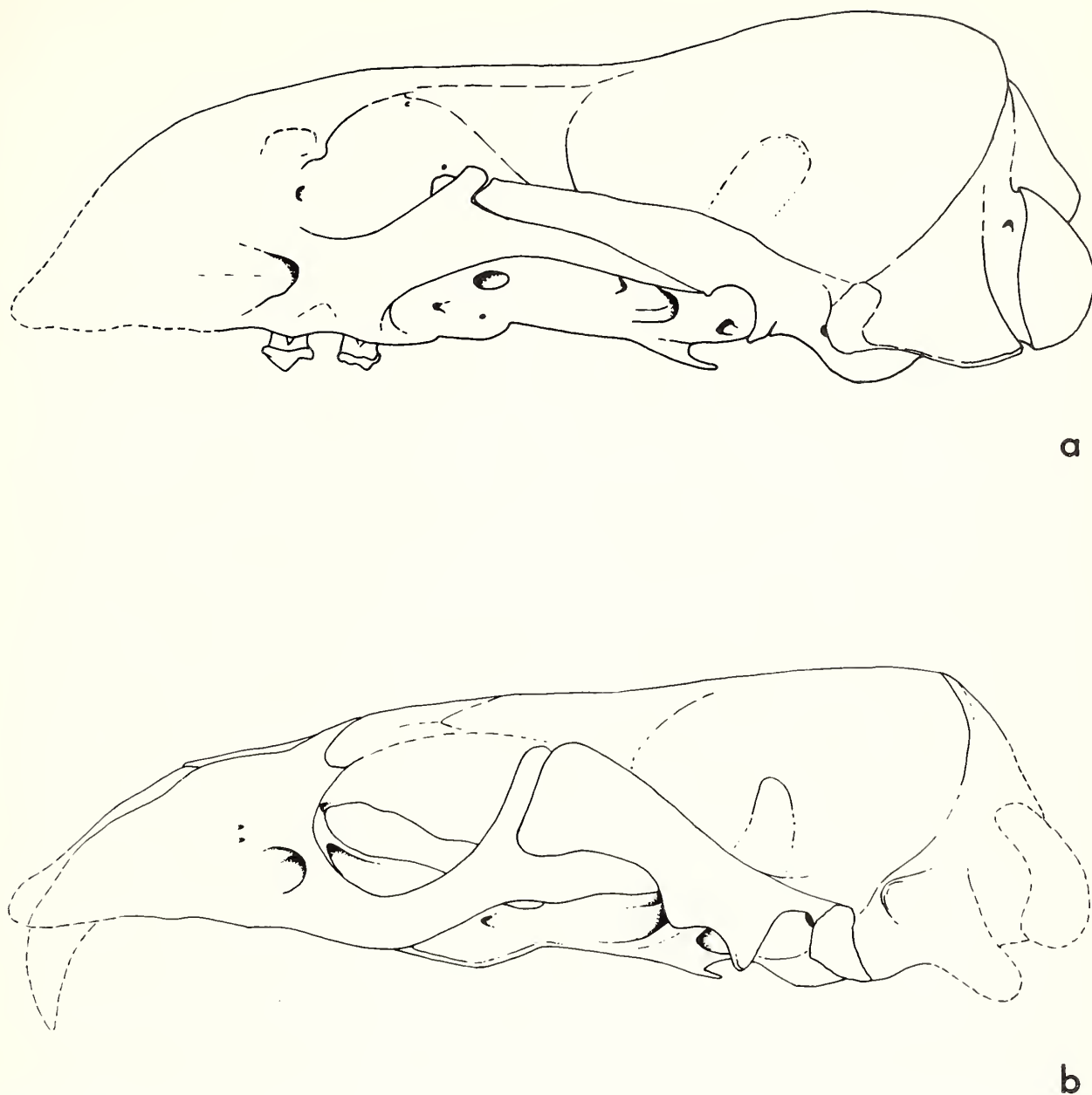


FIGURE 19. Restorations of skulls: *a*, *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334; *b*, *Allodesmus packardi* Barnes 1972, holotype, CAS 4371A; both left lateral views reduced to approximately the same cranium length. (*b* modified from Barnes 1972: figs. 21b, c.)

tor of *Desmatophoca* and *Allodesmus* was of late Oligocene or early Miocene age. I (Barnes 1972:fig. 25) once postulated a more recent common ancestry.

The cranial anatomy of *Desmatophoca oregonensis* has not been entirely described in detail, but Condon's (1906) description of the holotype has been supplemented by subsequently published information and illustrations (Mitchell 1966:36–37, pl. 29; 1968:1883, 1893–1894, table V; 1975:12–14, fig. 2; Repenning and Tedford 1977:74). By possessing three important, apparently derived characters, which it shares with *Allodesmus packardi* and/or with *A. kernensis*, *Pinnarctidion bishopi* differs from the holotype of *Desmatophoca oregonensis*. These are: the extreme

lateral excavation of the palatine-pterygoid strut between the palate and the brain case, the more dorsoventrally flattened posterior narial opening, and the more posterior and ventral position of the orbital aperture of the optic foramen. These differences suggest to me that the subfamily Allodesminae, now known mainly by species in the genus *Allodesmus*, was derived directly from the subfamily Enaliarctinae as it is defined in this report, and more specifically from species in the genus *Pinnarctidion*. Apparently *Desmatophoca oregonensis* could not have evolved from *Pinnarctidion bishopi* nor given rise to species of *Allodesmus* without there having been two reversals in the evolution of the three derived characters cited above. By this logic separate line-

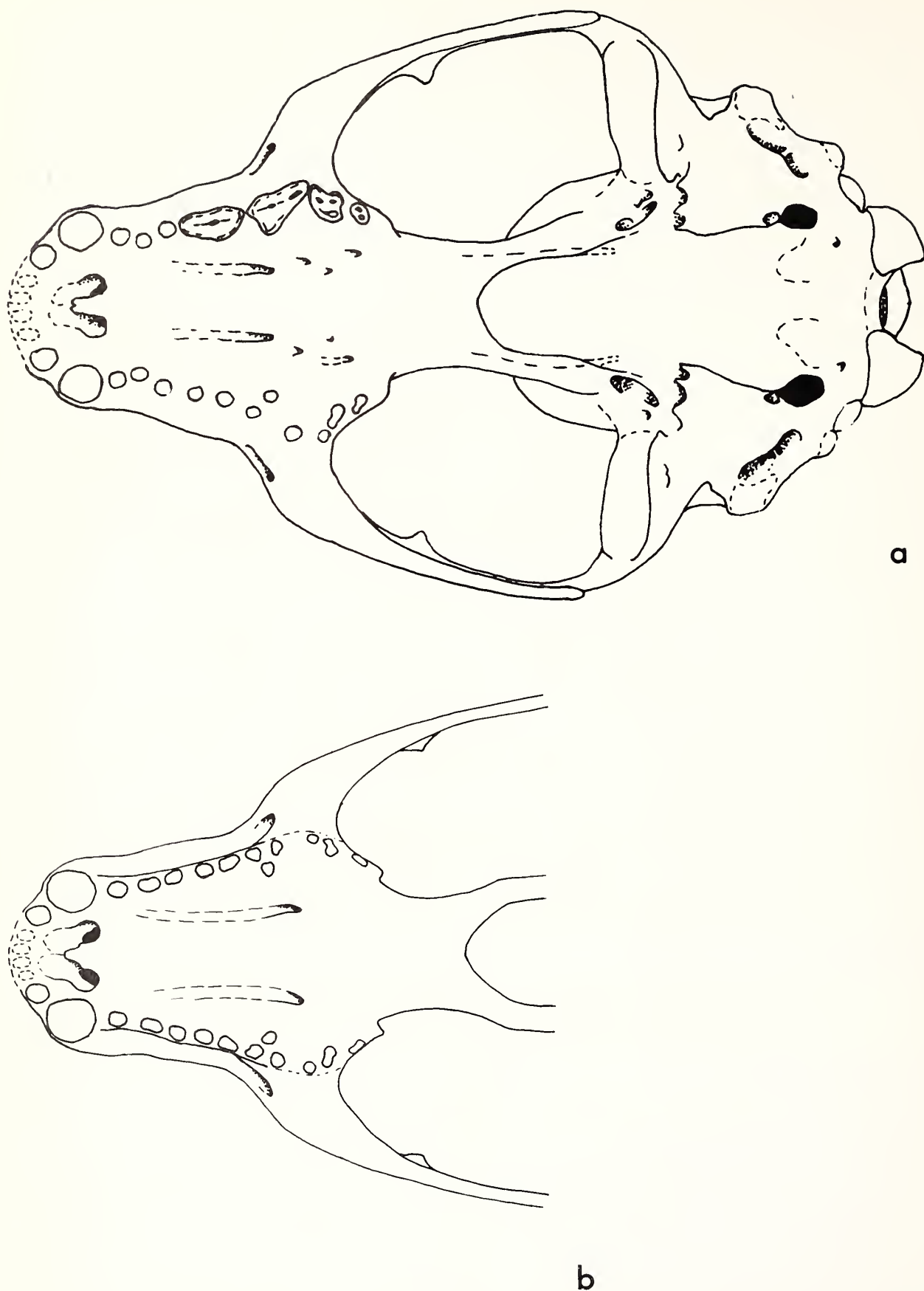


FIGURE 20. Restorations of skulls: *a*, *Enaliarctos mealsi* Mitchell and Tedford 1973, holotype, LACM 4321, and referred specimen, LACM (CIT) 5303, showing positions of cheek tooth alveoli on the right side; *b*, *Enaliarctos mitchelli*, new species, holotype, UCMP 100391, and paratype, UCMP 80943; both ventral views reduced to approximately the same cranium length. (*a* modified from Mitchell and Tedford 1973:figs. 5a, 12a, and 17c, with rostral extremity in part from *E. mitchelli*, new species.

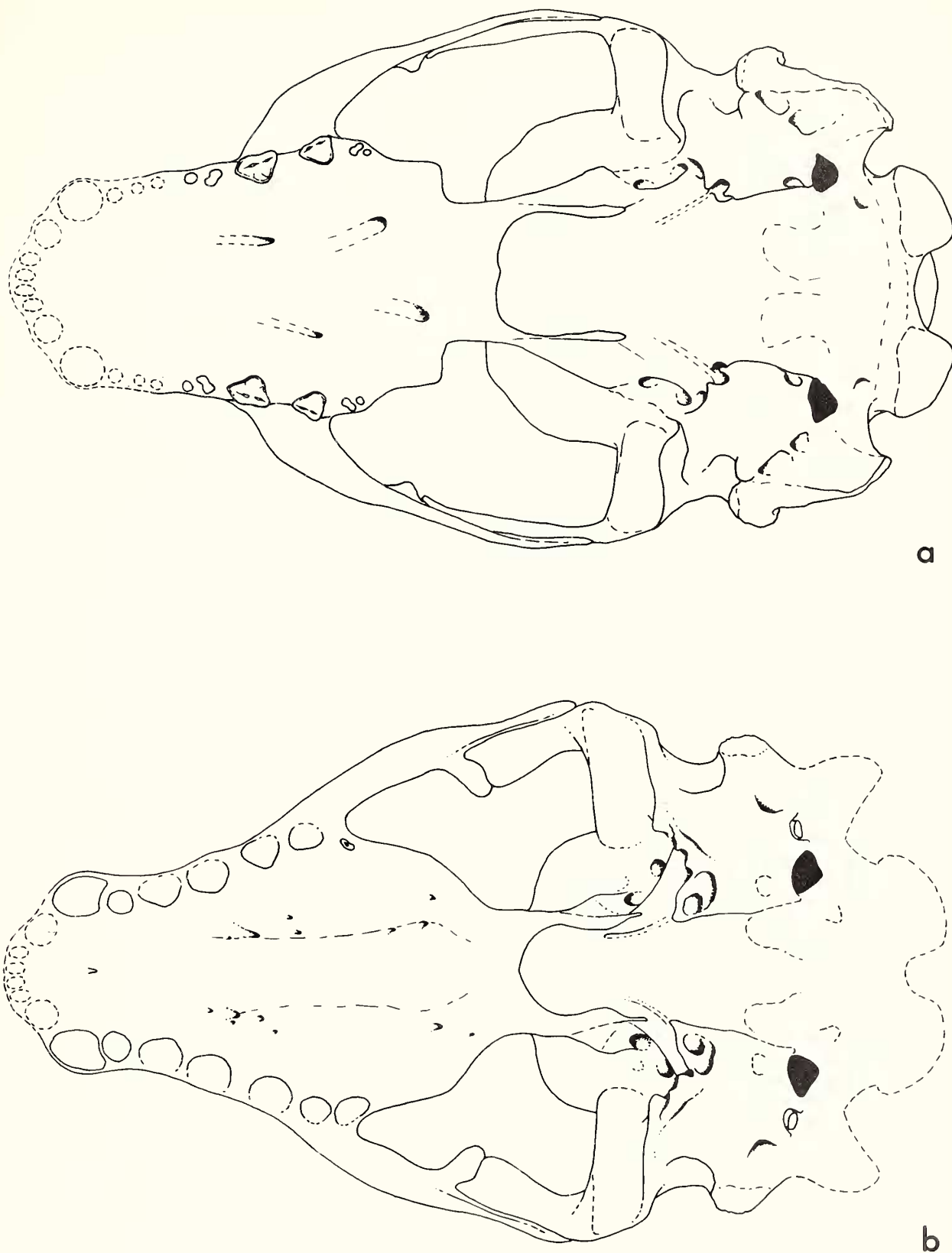


FIGURE 21. Restorations of skulls: *a*, *Pinnarctidion bishopi*, new genus and species, holotype, UCMP 86334; *b*, *Allodesmus packardi* Barnes 1972, holotype, CAS 4371A; both ventral views reduced to approximately the same cranium length. (*b* modified from Barnes 1972:fig. 19.)

ages (see Fig. 22) leading to the Allodesminae and the Desmatophocinae would extend back approximately 7 million years earlier than indicated by Repenning and Tedford (1977:fig. 6), at least to a time contemporaneous with *Pinnarctidion bishopi* between about 22 and 24 million years ago, if not before. The actual evolutionary divergence between the subfamilies Allodesminae and Desmatophocine would therefore be prior to about 22 to 24 million years ago as theorized by Mitchell (1968:1888).

Repenning and Tedford (1977:fig. 6) proposed a phylogeny in which *Enaliarctos mealsi*, at about 22 million years ago, was near the basal enaliarctine stock. From this basal stock they showed the subsequent evolution of three main derived groups. These are: 1) Otariinae (their Otariidae), 2) Desmatophocinae and Allodesminae (their Desmatophocidae), and 3) Imagotariinae and Odobeninae (their Odobenidae) (see also Repenning 1975:fig. 11). As partial evidence for this early diversification, Repenning and Tedford indicated that at least four unnamed species of enaliarctines lived between about 16 and 19 million years ago.

The phylogeny I present here (Fig. 22) suggests that the subfamilies Otariinae, Desmatophocinae, and Allodesminae were each independently derived from different species within the Enaliarctinae. I have accepted the arbitrary division between the Enaliarctinae and the derived groups as being the transition point between heterodont cheek teeth including carnassials and homodont cheek teeth (see Repenning 1975:fig. 11; 1976:377; Repenning and Tedford 1977). The similarities between species of Desmatophocinae and Allodesminae indicate that these subfamilies probably arose from species of enaliarctines that were more closely related than are *Enaliarctos* spp. and *Pinnarctidion bishopi*, or that they underwent convergent evolution. The origins of the Odobeninae and Imagotariinae are presently more obscure. Repenning and Tedford (1977:55) classified the middle Miocene *Neotherium mirum* Kellogg 1931 as a species of Dusignathinae. In my classification it would be a primitive species of Imagotariinae. My observations of *Neotherium mirum* (manuscript in preparation) indicate that it is not synonymous with *Enaliarctos mealsi*, *E. mitchelli*, or *Pinnarctidion bishopi*, but has some enaliarctine characters.

The present fossil sample size is small, but preliminary indications are that individuals of *Enaliarctos* spp. are more abundant than *Pinnarctidion bishopi* in the Pyramid Hill Sand Member of the Jewett Sand exposed at Pyramid Hill. *Enaliarctos mealsi*, *E. mitchelli*, and *Pinnarctidion bishopi* are each represented by two skulls and *E. mealsi* is represented by numerous additional isolated teeth.

Pinnarctidion bishopi was probably, although not undoubtedly, contemporaneous with *E. mitchelli*. Therefore, possibly at least two enaliarctine species were sympatric, but aspects of population dynamics and interspecific competition of enaliarctines cannot be dealt with at this time.

CLASSIFICATION OF THE OTARIIDAE

CLASS MAMMALIA Linnaeus 1758.

Order CARNIVORA Bowdich 1821.

Family Otariidae Gill 1866.

Subfamily Enaliarctinae Mitchell and Tedford 1973.

Enaliarctos Mitchell and Tedford 1973.

Enaliarctos mealsi Mitchell and Tedford 1973.

Enaliarctos mitchelli new species.

Pinnarctidion new genus.

Pinnarctidion bishopi new species.

Subfamily Desmatophocinae Hay 1930.

Desmatophoca Condon 1906.

"Desmatophocine A" of Barnes 1972.

Subfamily Allodesminae Kellogg 1931.

Allodesmus Kellogg 1922.

"Desmatophocine B" of Barnes 1972.

"Desmatophocine C" of Barnes 1972.

Subfamily Imagotariinae Mitchell 1968.

Neotherium Kellogg 1931.

Imagotaria Mitchell 1968.

Pontolis True 1906.

Subfamily Odobeninae Allen 1880.

Dusignathus Kellogg 1927.

Pliopedia Kellogg 1921.

Aivukus Repenning and Tedford 1977.

Prorosmarus Berry and Gregory 1906.

Alachtherium Du Bus 1867.

Trichecodon Lankester 1865.

Odobenus Brisson 1762.

Subfamily Otariinae Gill 1866.

Pithanotaria Kellogg 1925.

Thalassoleon Repenning and Tedford 1977.

Arctocephalus Geoffroy and Cuvier 1826.

Callorhinus Gray 1859.

Zalophus Gill 1866.

Eumetopias Gill 1866.

Neophoca Gray 1866.

Phocarctos Peters 1866.

Otaria Péron 1816.

Otariidae, *incertae sedis*:

Oriensarctos Mitchell 1968.

Valenictus Mitchell 1961.

CONCLUSIONS

1. The eared seals, including sea lions, fur seals, walruses, and their fossil relatives are best classified in one family, the Otariidae, in the mammalian order Carnivora. In the Otariidae, I recognize six subfamilies: Enaliarctinae, Desmatophocinae, Allodesminae, Imagotariinae, Odobeninae, and Otariinae. This

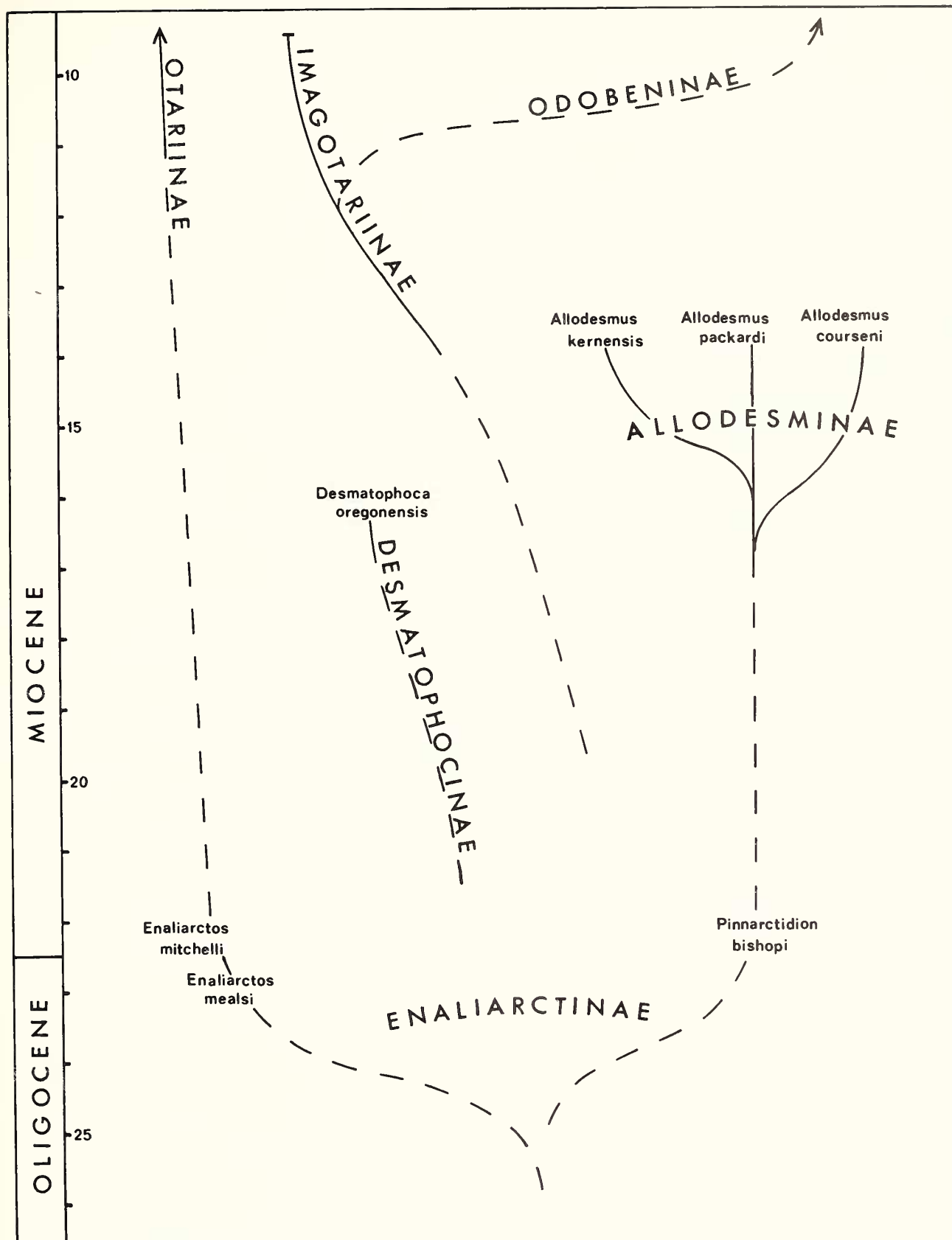


FIGURE 22. Suggested phylogeny of early enaliarctine otariids showing possible relationships to derived taxa. Dashed lines depict implied but uncertain relationships not yet documented by the known fossil record. Arrows indicate lineages that continue to present time. The positions of *Enaliarctos mealsi*, *E. mitchelli*, and *Pinnarctidion bishopi* are approximate relative to the time scale, but the positions of all indicated species are correct relative to one another based upon present stratigraphic information.

classification unites related animals into a single family having numerical and morphological diversity that is comparable with some other families of Carnivora.

2. The subfamily Enaliarctinae is the most primitive of these subfamilies and is apparently directly or indirectly ancestral to all the others. This subfamily contains three described species in two genera presently represented by fossils from the lower part of the Pyramid Hill Sand Member of the Jewett Sand which is exposed on the south face of Pyramid Hill in Kern County, California. These fossils are latest Oligocene to earliest Miocene in age, are correlated with the Arikareean North American land mammal age, the late Zemorrian or early Saucanian foraminiferal stages, and the "Vaqueros" provisional provincial marine megafaunal stage, and are, therefore, approximately 22 to 24 million years old.

3. The most primitive known genus of Enaliarctinae is *Enaliarctos* Mitchell and Tedford 1973. No new evidence contradicts previous suggestions that *Enaliarctos* may be involved in the ancestry of the derived subfamily Otariinae, which includes modern fur seals and sea lions.

4. The most primitive species of *Enaliarctos* is *E. mealsi* Mitchell and Tedford 1973. A new species, *Enaliarctos mitchelli*, is more derived than *E. mealsi*, was probably more specialized for aquatic existence, apparently had reduced carnassial function of the cheek teeth, and its source was probably from a higher stratigraphic level within the Pyramid Hill Sand Member than the beds that produced *E. mealsi*.

5. Another, very different enaliarctine is the more aquatically adapted *Pinnarctidion bishopi*, new genus and species. Its holotype is a fossil skull that was collected from rocks stratigraphically higher in the Pyramid Hill Sand Member than the probable source of specimens of *Enaliarctos mealsi*. The specimens of *Enaliarctos mitchelli* were probably derived from the same higher bed that produced *P. bishopi*, and the two species were probably contemporaries. It is not known whether these two species inhabited the same area simultaneously or whether differing migratory patterns separated their populations.

6. *Pinnarctidion bishopi* shares some primitive characters with *Enaliarctos mealsi* and *E. mitchelli*. It also shares many other characters, some of which appear to be derived, with middle Miocene species of the genus *Allodesmus*, and is therefore possibly ancestral to the subfamily Allodesminae. Some of the characters shared by *Pinnarctidion bishopi* and *Allodesmus* spp. are not present in *Desmatophoca oregonensis* of early middle Miocene age, and the latter species is therefore probably not an ancestor of *Allodesmus* spp. as has been previously suggested. This apparent dichotomy between the two lineages that led to *Desmatophoca oregonensis* and to *Allodesmus* spp. is older than has been previously suggested by some authors. This reinforces some other published arguments based on morphology that the nominal subfamilies Desmatophocinae and Allodesminae should be classified separately. Current evidence suggests, therefore, that these two subfamilies could only have shared a common ancestry prior to the existence of *Pinnarctidion bishopi* which lived between approximately 22 and 24 million years ago.

7. The anterior narial opening and other characters of *Enaliarctos mitchelli* are developed in ways indicating convergent evolution with some modern true seals of the family Phocidae. Examples of convergence between species of Phocidae and Otariidae have been pointed out by various authors, and it is significant that the phenomenon existed even among the earliest of

fossil otariids.

8. Mostly unpublished fossil evidence, including data on sharks, indicates that the two fossiliferous concretion-bearing beds at Pyramid Hill in the basal part of the Pyramid Hill Sand Member of the Jewett Sand contain different fossil vertebrate species. The existence of different pinniped species (*Enaliarctos mealsi* apparently in the lower bed, *E. mitchelli* and *Pinnarctidion bishopi* in the upper bed) in the two beds bolsters the probability that they differ substantially in age and/or environment of deposition. The Pyramid Hill Local Fauna, as defined by Mitchell and Tedford (1973), should therefore be strictly limited to the fossil assemblage from the basal "grit zone" of the Pyramid Hill Sand Member. The only specimen that Mitchell and Tedford (1973) assigned to the Pyramid Hill Local Fauna and which I would not, is the isolated matrix endocranial cast which they referred to *Enaliarctos mealsi* and which I have referred to *Pinnarctidion bishopi*, the species whose holotype is known to have been collected from the upper bed. The fossil assemblage from the upper bed, therefore, merits a separate local fauna name. I recommend that it not be named, however, until the assemblage is identified and the origin of the possibly redeposited bone-bearing concretions is investigated.

9. One other locality, at Point Arena in northern California, has produced a mandible tentatively identified as *Enaliarctos* sp. It is from the Skooner Gulch Formation of early Miocene age.

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